Ó Gogáin, A., Falcon-Lang, H. J., Carpenter, D. K., Miller, R. F., Benton, M. J., Pufahl, P. K., Ruta, M., Davies, T. G., Hinds, S. J., & Stimson, M. R. (2016). Fish and tetrapod communities across a marine to brackish salinity gradient in the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and their palaeoecological and palaeogeographical implications. *Palaeontology*, *59*(5), 689-724. https://doi.org/10.1111/pala.12249

Fish and tetrapod communities across a marine to brackish salinity gradient in the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and their palaeoecological and palaeogeographic implications

by AODHÁN Ó GOGÁIN[1, 2], HOWARD J. FALCON-LANG[3], DAVID K. CARPENTER[4], RANDALL F. MILLER[5], MICHAEL J. BENTON[1], PEIR K. PUFAHL[6], MARCELLO RUTA[7], THOMAS G. DAVIES[1], STEVEN J. HINDS[8] *and* MATTHEW R. STIMSON[5, 8]

[1] School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK; e-mails: ogogaina@tcd.ie; mike.benton@bristol.ac.uk; thomas.davies@bristol.ac.uk

[2] *Current address:* Department of Geology, Trinity College Dublin, Dublin 2, Ireland

[3] Department of Earth Sciences, Royal Holloway, Egham, Surrey, TW20 0EX, UK; e-mail: h.falcon-lang@es.rhul.ac.uk

[4] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton Waterfront Campus, European Way, Southampton, SO14 3ZH, UK; e-mail: dkc1g12@soton.ac.uk

[5] Natural Science Department, New Brunswick Museum, 277 Douglas Avenue, Saint John, New Brunswick, E2K 1E5, Canada; e-mails: Randall.Miller@nbm-mnb.ca, mstimson29@gmail.com

[6] Department of Earth and Environmental Science, Acadia University, Wolfville, Nova Scotia, B4P 2R6, Canada; e-mail: peir.pufahl@acadiau.ca

[7] School of Life Sciences, University of Lincoln, Green Lane, Lincoln, LN6 7DL, UK; e-mail: mruta@lincoln.ac.uk

[8] New Brunswick Department of Energy and Mines, Geological Surveys Branch, Fredericton, New Brunswick, E3B 5H1, Canada; e-mail: Steven.Hinds@gnb.ca

Abstract: Euryhaline adaptations in Pennsylvanian vertebrates allowed them to inhabit the marine to freshwater spectrum. This is illustrated by new assemblages of fish and tetrapods from the early Moscovian Minto Formation of New Brunswick, Canada. Fish include chondrichthyans (xenacanthids, and the enigmatic *Ageleodus*), acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids, megalichthyids and dipnoans), and actinopterygians (eurynotiforms). Tetrapods include small to medium-sized, and largely aquatic, stem tetrapods (colosteids) and anthracosaurs (embolomeres). A key finding is that the parautochthonous fossil assemblages are preserved across a salinity gradient, with diversity (measured by the Simpson Index) declining from open marine environments, through brackish embayments, and reaching a nadir in tidal estuaries. Chondrichthyans dominate the entire salinity spectrum (65% of fossils), a distribution that demonstrates a euryhaline mode of life, and one large predatory chondrichthyan, *Orthacanthus*, may have practised filial cannibalism in coastal nurseries because its heteropolar coprolites contain juvenile xenacanthid teeth. In contrast, other fish communities were more common in open marine settings while tetrapods were more common in coastal brackish waters. While all these faunas were, also, likely, euryhaline, their osmoregulation was, perhaps, less versatile. The demonstration of widespread euryhalinity among fish and aquatic tetrapods explains why Pennsylvanian faunas generally show a cosmopolitan biogeography because taxa were able to disperse via seaways. It also resolves the paradox of enriched strontium isotopic signatures observed in these faunas because organisms would have been, at times, exposed to continental water bodies as well. Therefore, our new findings contribute to the long-running debates about the ecology of Pennsylvanian fishes and tetrapods.

Key words: Pennsylvanian, fish communities, salinity gradient, euryhaline, cosmopolitan, New Brunswick.

EURYHALINE animals are relatively rare in modern ecosystems (Edwards and Marshall 2013; McCormick *et al.* 2013), with less than 10% of organisms adopting this osmoregulatory strategy (Schultz and McCormick 2013). In contrast, euryhaline adaptations appear to have been much more widespread at certain times in the geologic past (Minter *et al.* 2016), and, in fact, may have played a critical transitional role in the Palaeozoic colonisation of continental freshwater ecospace (Buatois *et al.* 1998; Miller and Labandeira 2002; Park and Gierlowski-Kordesch 2007; Falcon-Lang *et al.* 2015*a*). Adaptation to lower and more variably saline (brackish to fresh) water bodies commenced as early as the Ordovician (MacNaughton *et al.* 2002; Davies and Sansom 2009; Sansom *et al.* 2009), and the abundance and complexity of these ecosystems steadily increasing through the Silurian–Carboniferous (Jones and Dixon 1977; Buatois *et al.* 2005; Kennedy *et al.* 2012). Colonisation patterns closely parallel the Ordovician rise of hepatophytes and the Silurian–Carboniferous diversification of tracheophytes (Gensel and Edwards 2001), indicating co-evolutionary teleconnections between land plants, terrestrial-marine nutrient export patterns (Algeo and Scheckler 1998), and the carrying capacity of 'non-marine' coastal environments (Prescott *et al.* 2014).

Adoption of euryhalinity appears to have peaked during a "mid-Carboniferous diversification" when this mode of life, temporarily, became dominant (Davies and Gibling 2013; Falcon-Lang *et al.* 2015*a*) among organisms as diverse as microconchids, ostracodes, xiphosurans and fish (Anderson and Shuster 2003; Carpenter *et al.* 2011; Bennett *et al.* 2012; Gierlowski-Kordesch and Cassle 2015; Gierlowski-Kordesch *et al.* 2016), perhaps, in order to utilise depauperate non-marine coastal ecospace for feeding and breeding (Williams *et al.* 2006; Carpenter *et al.* 2014). Rapid diversification coincided with the sharp growth of Gondwanan ice sheets and the onset of significant Milankovitch-driven glacio-eustatic fluctuations (Fielding *et al.* 2008; Montañez and Poulsen 2013). These marine transgressions with magnitudes up to 120 m (Rygel *et al.* 2008) repeatedly flooded continental margins,

creating extensive epicontinental microtidal seaways (Wells *et al.* 2005), whose salinity slowly decreased in a landward direction over many hundreds of kilometres (Falcon-Lang 2005; Falcon-Lang *et al.* 2015*b*), similar to the present-day Baltic Sea (Andersson *et al.* 1992 1994). This palaeo-oceanographic context probably provided optimum conditions for euryhaline organisms to exploit brackish environments.

In this paper, we describe euryhalinity in Late Paleozoic vertebrate communities. Facies analysis suggests that a wide range of fish, including gyracanthids, elasmobranchs, dipnoans, rhizodonts and megalichthyids, as well as tetrapods, existed in freshwater to brackish environments in Devonian–Carboniferous times (Friedman and Sallan 2012; Schultze 2013), and much recent attention has been given to the apparent dominance of a euryhaline mode of life among mid-Carboniferous vertebrate communities (Schultze 2009; Carpenter *et al.* 2011, 2014, 2015). However, consensus regarding ecology is currently lacking, with some researchers arguing on palaeogeographic, sedimentological and geochemical grounds that fish taxa, especially xenacanthid sharks (Masson and Rust 1984), and tetrapods, may have been obligate freshwater organisms (Johnson, 1979, 1999; Štamberg and Zajíc 2008; Fischer *et al.* 2011, 2013; Montañez and Cecil 2013). In this paper, we describe a new fauna of fish and tetrapods from the Carboniferous (Pennsylvanian; early Moscovian) of New Brunswick, Canada (Fig. 1A), and demonstrate – based on independent indicators of palaeo-salinity – that certain fish and tetrapod taxa existed across a brackish to marine gradient, and that communities must therefore have been euryhaline. We discuss how these new findings improve understanding of Carboniferous fish and tetrapod ecology.

GEOLOGICAL CONTEXT

The fish and tetrapod fossils reported here were obtained from opencast mine sites (now reclaimed) within the Minto Coalfield, Queens County, New Brunswick, Canada (Fig. 1A–C).

100 The rocks of the Minto Coalfield are of historical interest, having been the first place in North
101 America where coal was mined, beginning in 1639, and they are mentioned in a 1667 entry of
102 Samuel Pepys' famous diary (Smith 1989; Falcon-Lang 2009; Quann *et al.* 2010).
103
104 *Stratigraphy, age and basin analysis*
105 Rocks of the Minto Coalfield belong to the Pennsylvanian Minto Formation (*sensu* St Peter
106 and Johnson 2009), the lowest unit of the Pictou Group. They were deposited on the New
107 Brunswick Platform (Fig. 1B–C), a stable cratonic region that lay to the north of the oblique
108 collisional zone between Laurasia and Gondwana (Gibling *et al.* 2008). Based on combined
109 megafloral and palynofloral biostratigraphy, the Minto Formation is thought to be latest
110 Duckmantian to Bolsovian in age (Hacquebard and Barss 1970; St Peter 1997, 2000), with the
111 economically important Minto Coal specifically dated as early Bolsovian (Kalkreuth *et al.*
112 2000). Radiometric ages recently obtained from immediately below and above the Aegiranum
113 Marine Band, which marks the Duckmantian–Bolsovian in western Europe (Pointon *et al.*
114 2012; Waters and Condon 2012), suggest an age of c. 314 Ma for this boundary. The Minto
115 Formation therefore correlates with the early part of the Moscovian Stage (Peterson 2011;
116 Richards 2013; Fig. 2A).
117 Within the Minto Coalfield, sediments of the Minto Formation were deposited
118 unconformably over the top of basement rocks of Mississippian age and older, as the cratonic
119 New Brunswick Platform underwent thermal subsidence (Gibling *et al.* 2008; Fig. 2B).
120 Extensive borehole arrays indicate that this basal unconformity is marked by a major silcrete
121 palaeosol, up to 9 m thick in places (Sullivan 1981; St Peter 2000), which mantles the
122 basement complex and indicates seasonally dry-climate weathering over the preceding several
123 million years of depositional hiatus (St Peter and Johnson 2009). In the course of this lengthy
124 episode of landscape degradation, a NE-SW-trending valley system, c. 16 km wide, was cut

into the basement, forming an erosional 'container' (degradational depocentre) in which younger sediments of the Minto Formation accumulated (Hacquebard and Barss 1970).

This bedrock palaeovalley was bordered on either side by slates and lavas that formed subdued topographic highs with a palaeo-elevation of a few tens of metres above base level (Hacquebard and Barss 1970; Gray *et al.* 2012; Fig. 3A). Two lines of evidence suggest that the valley drained towards the southwest (Hacquebard and Barss 1970): (1) the thickness of the lower part of the formation, as measured from the basement contact to the base of the Minto Coal (a prominent chronostratigraphic marker bed) gradually increases from c. 15 m in northeast to > 90 m in the southwest (Fig. 3A), implying that the basin deepened towards the southwest, and sediment progressively onlapped towards the northeast; and (2) NE-SW-orientated ribbons of channelized sandstone, 1–1.5 km wide, in the 'roof rock' of the Minto Coal, fine towards the southwest (Fig. 3B) and suggest sediment transport in that direction. We note, however, that this inferred palaeoflow direction opposes regional patterns of sediment dispersal, which are directed towards the ENE (van de Poll 1973; Gibling *et al.* 1992). This suggests that either drainage in the Minto Coalfield was strongly influenced by local bedrock topography, or that palaeoflow inferences based on grain size and isopachytes are incorrect. More reliable palaeoflow indicators, such as cross-bed arrays, have not been obtained to date due to poor surface exposure.

Palaeoenvironments

Despite its long history of geological study (Gesner 1841; Robb 1850; Bailey and Matthew 1873), there have been no comprehensive studies of the sedimentary facies of the Minto Formation (St Peter 2000; Clark 2004; St Peter and Johnson 2009). Three units are generally recognised, and their lithologies are described below, based on our own studies of borehole

149 cores (DH62-1 to 3) accessioned at the New Brunswick Department of Energy and Mines,
150 Geological Surveys Branch, Fredericton (Fig. 4A).

151 The lowest unit, up to 60 m thick (uppermost part only is shown in Fig. 4A),
152 comprises quartz pebble and intraclast conglomerate, fine- to very coarse-grained trough
153 cross-bedded sandstone, and grey siltstone arranged in fining-upward successions, with
154 intermittent silcrete palaeosols. These beds resemble the broadly coeval (early Moscovian)
155 South Bar Formation of Nova Scotia, which formed under braided fluvial conditions (Rust
156 and Gibling 1990), and the early Moscovian Waddens Cove Formation of Nova Scotia, which
157 shows similar silcrete palaeosols (Gibling and Rust 1992). The beds are interpreted as the
158 fluvial channel deposits of a poorly- to well-drained coastal plain.

159 The middle unit, up to 15 m thick (Fig. 4A), comprises grey laminated shale with
160 distinctive 'pinstripe' laminations of very fine-grained to fine-grained sandstone. Sedimentary
161 structures include ripple cross-lamination showing mud drape pairs, flaser bedding, and
162 symmetrical ripples (Fig. 4B–C). At one level is developed the < 0.8 m thick Minto Coal,
163 underlain by a seat earth, 1 m thick (rooted, bleached palaeosol). These beds resemble those of
164 the broadly coeval (early Moscovian) Malagash Formation of Nova Scotia, interpreted as tidal
165 deposits (Naylor *et al.* 1998; Costain 2000), with the coal being formed in a calamite-
166 dominated coastal peat mire (Kalkreuth *et al.* 2000). Proximity of the peat mire to an open
167 brackish-marine embayment is supported by the relatively high (5–9%) sulphur content of the
168 Minto Coal, which increases towards the southwest and the basin centre (Fig. 3A; Hacquebard
169 and Barss 1970). Sandstone ribbons, up to 1.5 km wide, that have been mapped in the
170 succession overlying the Minto Coal, and locally 'wash out' the coal (Fig. 3B) may represent
171 incised valleys, flooded to form tidal estuaries; however, this interpretation cannot be
172 confirmed because the boreholes do not intersect this facies.

The uppermost unit, c. 100 m thick (lowermost part only shown in Fig. 4A), comprises units of pebbly sandstone, thin sandstone sheets, and relatively thick intervals of massive, red mudrock, locally showing slickensides and small, scattered carbonate nodules. These beds were formerly assigned to the Hurley Creek Formation, but were amalgamated into the Minto Formation by St Peter (2000), based on regional mapping. The succession probably represents the deposits of a relatively well-drained alluvial plain (cf. Davies and Gibling 2003), but borehole characteristics are insufficient for detailed analysis.

Fish- and tetrapod-bearing lithologies

Fish and tetrapod assemblages reported here were not collected *in situ* within a logged succession, but obtained from the tip heap piles of opencast mines exploiting the Minto Coal at relatively shallow depth, and must have come from the overburden of the coal. A careful review of all fossiliferous specimens shows that the fossils occur in four different lithologies, and can be related to the logged section, with varying degrees of confidence. All fossils are inferred to have come from the middle unit (tidal/estuarine facies), as shown on Fig. 4A.

Lithology 1 comprises a medium grey limestone bed, up to 24 mm thick, which shows abundant fish skeletal fragments throughout. In petrographic thin section, the lithology comprises a wackestone containing scattered bioclasts of punctate brachiopods (Fig. 5A, D), fish bones (Fig. 5B), ostracodes (Fig. 5C), putative sponge spicules (Fig. 5D), spirorbiform microconchids (Fig. 5E), echinoid spines (Fig. 5F), and putative forams (Fig. 5G). An early diagenetic phase of framboidal pyrite (Fig. 5F) commonly infills voids, followed by a later phase of sparry calcite (Fig. 5C, E, G). The only macroscopic invertebrate fossils that are visible in hand specimen are rare spirorbiform microconchids. The invertebrate assemblage, together with the presence of framboidal pyrite, indicates deposition under fully marine conditions (Maliva 1989; Tucker and Wright 1990; Schieber 2002). The high micrite content

198 indicates quiet bottom waters, and the absence of siliciclastic grains suggests that the marine
199 embayment was relatively extensive (Gibling and Kalkreuth 1991). Similar marine limestone
200 beds have been documented elsewhere in the Maritimes Basin, in the Pennsylvanian
201 (Langsettian) Joggins Formation (Grey *et al.* 2011) and Tynemouth Creek Formation (Falcon-
202 Lang *et al.* 2015*a*).

203 Lithology 2 comprises dark grey, bituminous limestone, up to 28 mm thick, showing
204 abundant fragments and rare articulated examples of the bivalve *Naiadites* (Fig. 6A),
205 spirorbiform microconchids (Fig. 6B-C), and a large quantity of comminuted fossil plant
206 debris. In petrographic thin section, these lithologies comprise bivalve-dominated packstone
207 with minimal micrite matrix (Fig. 5H–I), rare fish fragments (Fig. 5I) and spirorbiform
208 microconchids. Calver (1968) interpreted *Naiadites* as a mostly brackish bivalve, and it is
209 known also from identical lithologies in the Pennsylvanian Joggins, Port Hood, Parrsboro, and
210 Sydney Mines Formations of nearby Nova Scotia, where they have been interpreted as the
211 deposits of extensive brackish embayments (Gibling and Kalkreuth 1991; Calder 1998;
212 Falcon-Lang *et al.* 2006). The environment was probably shallow and wave-agitated given
213 that the micrite matrix has largely been winnowed away and bivalves are commonly
214 fragmented (Davies and Gibling 2003; Falcon-Lang 2005; Carpenter *et al.* 2015).

215 Neither limestone lithology was observed in the logged boreholes. However, in the
216 Joggins Formation of Nova Scotia, such thin limestone beds form the roof of coal seams
217 (Davies and Gibling 2003; Falcon-Lang 2005), and represent brackish-marine flooding
218 surfaces, possibly triggered by glacio-eustatic or tectonic factors (Falcon-Lang *et al.* 2006). In
219 all the boreholes that we studied, the interval containing the Minto Coal has been removed for
220 coal petrographic analysis, and possibly with it, evidence for the stratigraphic position of
221 overlying limestone beds. Clearly, the two limestone lithologies represent open-water facies,
222 and the presence of comminuted plant debris in Lithology 2 suggests proximity to coastal

vegetation. Based on fossil content and lithology, we infer that Lithology 1 was formed in the offshore marine part of the embayment and Lithology 2 represents the coastal embayed zone where fluvial discharge led to lower and most variable salinities.

Lithology 3 comprises thinly bedded, pale grey siltstone to very fine-grained sandstone showing symmetrical ripple marks with mud drapes (Fig. 7A). In thin section, it shows a poorly developed micritic matrix. Fish skeletal fragments, included xenacanthid teeth, are particularly concentrated within the mud-rich ripple troughs (Fig. 7B). Lithology 4 comprises a medium- to dark-grey, laminated mudstone, with thin partings of very fine-grained sandstone, and isolated fish fragments. These latter two lithologies are identical to those found in the tidal/estuarine facies reported from the borehole core overlying the Minto Coal, and therefore can be directly related to the logged succession with a high degree of confidence. These clastic beds probably represent the most proximal of the fossiliferous lithologies, probably deposited within a tidal estuary developed on the coast of the brackish-marine epicontinental sea represented by the limestone beds.

MATERIAL AND METHOD

All fossil material reported here was obtained by surface prospecting on weathered tip heaps adjacent to back-filled opencast coal mines within the Minto Coalfield (Fig. 8), and no material was directly obtained in a sedimentary context.

Institutional abbreviation. NBMG, New Brunswick Museum (Geology), Saint John, New Brunswick, Canada.

Localities, collections and collections history

Fossil material was collected in four phases. Prior to 1988, William H. Forbes obtained 28 specimens from various sites in the Minto Coalfield, but without detailed locality data (Miller and Forbes 2001). Between c. 1991 and 2000, amateur palaeontologist Michael Lee obtained a much larger collection at Iron Bound Cove (Latitude 46°08.67'N; Longitude 65°58.10'W) and Coal Creek (Latitude 46°06.09'N; Longitude 65°53.39'W) on the Northeast Arm of Grand Lake, c. 10 km NE of Minto, Queens County (Fig. 1B–C). Those collections were augmented by one of us (RFM) in collaboration with Michael Lee, at Iron Bound Cove in 2002, and by three of us (AÓG, RFM, MRS) at Iron Bound Cove in 2015. There are 404 catalogued hand specimens from Iron Bound Cove and 60 catalogued hand specimens from Coal Creek, together with a further 230 specimens from Coal Creek that are currently uncatalogued but show indeterminate fish skeletal material only.

Specimen preparation and imaging

Fossils visible on bedding surfaces were prepared through a combination of mechanical and chemical removal of surrounding matrix. Mechanical preparation was by means of a pin-vice, assorted fine-tipped brushes, and tweezers. Where the matrix was too hard for this to work, specimens were immersed in a 5% acetic acid solution, buffered with calcium acetate, following the approach of Jeppsson *et al.* (1985). To minimise risk of fracture and to provide a barrier against acid attack, fossils were coated with a weak, ethanol-based contact adhesive ('Mowital') before acid digestion. Specimens prepared in this way were photographed with a Nikon D700 digital SLR camera with a Nikon 60 mm macro lens. Other specimens were photographed using a Panasonic Lumix DMC-ZS3 digital camera or a Canon Eos 40D digital camera using a Canon Ultrasonic 100mm macro lens or mounted on a Leica MS5 microscope. Figures were prepared with Adobe Photoshop Illustrator in Creative Suite 5.

SYSTEMATIC PALAEONTOLOGY

A comprehensive review of 722 hand specimens containing > 2692 individual fish skeletal fragments in the NBMG collections from the Minto Formation is given in the supplementary material (see Ó Gogáin *et al*. 2016, S1). Miller (1999) published a preliminary list of taxa known up to that date, but no detailed study of the material has been undertaken hitherto. We present the materials in the sequence Chondrichthyes, Acanthodii, Sarcopterygii, Actinopterygii (Table 1).

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Superorder XENACANTHIMORPHA Nelson, 1976

Order XENACANTHIFORMES Berg, 1937

Family DIPLODOSELACHIDAE Dick, 1981

Genus *ORTHACANTHUS* Agassiz, 1843*a*

Type species. Orthacanthus cylindricus Agassiz, 1843*a*

Orthacanthus compressus Newberry, 1856

Figure 9A–D

Material. 71 specimens bearing isolated teeth (NBMG 9948, 10740 (juvenile specimen attached to *Ctenodus* tooth plate), 10746–10748, 10757, 14953–14965, 14967–14968, 14983–14984, 14991–14993, 14996, 15823, 15825, 15832–15834, 15836, 15838, 15841, 15843, 15846–15847, 15849, 15902–15903, 15905–15910, 15916, 16088, 16090, 16093, 16095, 19614–19626, 19850, 19852–19854, 19856).

Diagnosis. Teeth bi- or tricuspid, with two lateral cusps flanking a median cusp in tricuspid teeth. Where present, the median cusp is smaller than the lateral cusps. Carinae may be present on the edges of the lateral cusps. Tooth base is thin with a round to oval shape. A

297 coronal button is present which does not contact any cusps. A median foramen is present on
298 the labial side of the coronal button. A basal tubercle may be present, which extends in a
299 labial direction and has a bulbous shape.
300 *Description.* Teeth range in height, as measured from the basal surface to the apex of the
301 largest cusp, from 0.5 to 11.0 mm (Fig. 10A). In larger teeth (> 1 mm) one lateral cusp is
302 typically larger than the other with both showing a degree of lateral divergence; the 'major
303 cusp' tends to diverge more than the 'minor cusps' (Fig. 9A–C), with some 'minor cusps'
304 having near vertical orientations. Lateral cusps have a lanceolate cross section. Carinae are
305 present on lateral cusps ≥ 1 mm. Serration is absent from all specimens. Median cusps,
306 although present in the majority of specimens, are absent in several teeth. The median cusps
307 of teeth > 0.5 mm high are on average less than 1/3 the height of associated lateral cusps,
308 whereas the median cusps of teeth ≤ 0.5 mm high are roughly the same height as the lateral
309 cusps. A median foramen is present in all specimens. The shape of the coronal button is
310 variable, and may be rounded, oval or heart-shaped (Fig. 9D), and oval coronal buttons are
311 elongated along the labial-lingual axis. Lingual to the coronal button are 1–4 nutritive
312 foramina except in one specimen where the button is absent; the precise placement of the
313 nutritive foramina varies between teeth. The bases of the teeth vary in shape from circular to
314 oval and have a 'scarred' appearance. Oval bases may be either elongated along the labial-
315 lingual axis or along the lateral axis. Base thickness shows a positive linear correlation with
316 base length and tooth height (R^2 = 0.8132, 0.816 respectively). A convex basal tubercle is
317 present in some specimens and forms a bulbous shape, which protrudes beyond the labial
318 margin of the base.
319 *Remarks.* Tooth size is unimodal (Fig. 10A), suggesting we have a single population and a
320 single species. Assigning small teeth and teeth which lack serration to the genus *Orthacanthus*
321 has been argued against by Hampe (1988). Johnson (1999), on the other hand, shows that

Orthacanthus teeth can lack serration and have small sizes. It is difficult to distinguish *Orthacanthus compressus* from *Orthacanthus texensis*; *O. texensis* has been ruled out as a possible identity here, as teeth of this species typically have thicker bases, whereas *O. compressus* teeth are characterised by having thin bases, although this is not always the case (Johnson 1999). Also our specimens lack serration, whereas serration has been recorded in thin-based teeth of *O. texensis* (Johnson 1999). Based on the placement of teeth within the jaw for *O. texensis* (Johnson 1999), it is reasonable to assume a posterior curvature of the 'major cusp' in the teeth of *O. compressus*.

Xenacanthiformes indet.

Figure 9E

Material. 32 specimens containing isolated teeth (NBMG 14966, 14985–14987, 14994, 15835, 15837–15838, 15842, 15848, 16082, 16089, 18613, 19628–19645).

Diagnosis. Bicuspid or tricuspid teeth with a base that extends lingually.

Description. Bi- or tricuspid teeth with a base that extends in a lingual to anterio-lingual direction. Cusps are lanceolate to oval in cross section and lateral cusps larger than 1 mm often have carinae on their lateral edges. Serration is absent in all specimens. A sub-circular coronal button is present in specimens with intact bases. In specimens not obscured by sediment there is no median foramen. A convex basal tubercle is present except where it has been broken off (Fig. 9E).

Remarks. The specimens are too fragmentary to identify beyond ordinal level. Some show individual features consistent with *Orthacanthus compressus*, such as the presence of carinae, but have not been included within *O. compressus* as these characteristics are shared by *Xenacanthus* (Johnson 1999).

Elasmobranchii indet.

Figure 9F–G

Material. 32 specimens containing 607 isolated scales (NBMG 19646–19677). Note that some of these specimens were obtained through the destructive dissolution of NBMG 14984, 15834, and 15901, and then assigned new collection numbers.

Diagnosis. Scales with thin bases and cusps extending out from the free-face. Scales vary from polycuspid to fused cusps.

Description. Scales range from ≤ 0.5 mm to ≤ 0.2 mm in both diameter and height (height measured from the base outwards along the denticles). The base of the scales is thin and tends to be dotted with holes, which are likely to be a result of post-mortem degradation, as hole morphology is highly variable. Cusps range from polycuspid to fused cusps, which form a robust structure (Fig. 9F). The cusps of the polycuspid scales tend to have a degree of curvature, and all curve in the same direction.

Remarks. Elasmobranch scales from the Palaeozoic have been shown to have a high degree of morphological variability, depending on which part of the body they are from (Dick 1981). This variability can be more pronounced than that seen between species, making the assignment of scales a difficult task. The Minto specimens show similarities to denticles depicted by Lebedev (1996, fig 6d–f), characterised there as "*Ctenacanthus*" type denticles (Karatajute-Talimaa 1992; Lebedev 1996).

Order *incertae sedis*

Family *incertae sedis*

Genus *AGELEODUS* Owen, 1867

Type species. Ageleodus pectinatus Agassiz, 1843*a*

Ageleodus pectinatus Agassiz, 1843*a*

Figure 9H–J

Material. 67 specimens containing isolated teeth (NBMG 9973b, 10800, 12067, 14965, 14969–14982, 14995, 14997–15004, 15175, 15806, 15838, 15858–15861, 15863, 15868, 15890–15893, 15895, 15897–15900, 16070–16072, 16095, 19600–19613, 19717, 19851).

Diagnosis. Mesio-distally elongated teeth with multiple sharp-conical cusps arranged in a row along the crown. The base is long, narrow and deep, and lacks imbrications.

Description. The teeth are mesio-distally elongated, giving an impression of anterior-posterior compression: the crown is bulbous on one side and flattened on the opposite side (Fig. 9H–J). The number of cusps on the crown varies from 9–18 (Fig. 10B) in complete specimens, with the exception of NBMG 15715, which has 35 (Fig. 9J). The cusps are sharp-conical, except where rounded by abrasion, and are situated along the crown, with 1–2 marginal cusps in a slightly ventral position at each edge. The root of the tooth is compressed and is punctuated by nutritive channels.

Remarks. As *A. pectinatus* is known only from disarticulated teeth, the arrangement of dentition within the jaws is unknown; we follow the terminology established by Downs and Daeschler (2001). Cusp count appears to be continuous and unimodal within the sample, with a mean of 14, and all specimens lie within the first standard deviation except for NBMG 15175 (Fig. 10B). This is similar to the variation in other samples (e.g. Downs and Daeschler 2001, fig. 3); in that example, the majority of specimens had 3 to 16 cusps, though rare teeth with as many as 33 cusps were found. Given the much smaller sample size here, the fact that specimens from Minto show less variation than those from Red Hill is not surprising; nonetheless, all specimens except NBMG 15715 fall within the range of variation established by Downs and Daeschler (2001) for *A. pectinatus*. Controversy continues to surround the interpretation and affinity of *Ageleodus* (Turner 2013). Here we have followed the conservative view that these features represent the teeth of a basal elasmobranch of uncertain

placement; however, we note that Lebedev (1996) proposed a rather different hypothesis, i.e., that they are not teeth at all, but rather specialised branchial denticles.

Class ACANTHODII Owen, 1846

Order *incertae sedis*

Family GYRACANTHIDAE Woodward, 1906 emend. Warren *et al.,* 2000

Genus *GYRACANTHIDES* Woodward, 1906

Type species. Gyracanthides murrayi Woodward, 1906

Gyracanthides sp.

Figure 11A–F

Material. One specimen containing 11 individual spine fragments (NBMG 10739/1–11) and two further specimens containing single spines (NBMG 10736, 15173, 15826, 19969, 19970).

Diagnosis. Laterally compressed spines with a V- to U-shaped cross section. Striated insertion area with an exsertion area covered by tubercles that form ornament ridges. Ornament ridges intersect in a chevron arrangement along the leading edge. Ridges are oblique to the long axis near the insertion area, but become parallel to the long axis towards the distal end in pectoral spines. This is not seen in dorsal and pelvic spines, where tubercle ridges are consistently oblique towards the distal end.

Description. NBMG 15173 is a partially exposed spine 84 mm long. The long axis shows a very small degree of curvature (Fig. 11A). The cross section of the spine does not show curvature, but this may be a result of the sediment obscuring parts of the spine. The insertion/ exsertion boundary (IEB; Fig. 11A) is hard to distinguish due to the high degree of abrasion on the ornament ridges. There is an angle of 42^{o} between the IEB and the ornamented ridges and 25^{o} between the IEB and the striae. Ornament ridges more distal to the IEB show less abrasion, allowing individual ridges to be traced, but the damage is still sufficient that

419 individual tubercles on the ridges are heavily worn and difficult to discern. Seven ridges cross
420 a line drawn perpendicular to the leading edge at the posterior limit of the insertion area (Fig.
421 11A, cf. Turner *et al.* 2005, fig. 2a).

422 NBMG 10739 is composed of 11 fragments from several different spines. In NBMG
423 10739/1–2 the ornament ridges of the exsertion area are pinched out by the insertion area
424 along the leading line (Fig 11B–C). Specimens NBMG 10739/1–2 measure 46 mm and 44
425 mm along their long axes respectively, with broken surfaces on the distal and proximal ends.
426 The cross-sectional shape of NBMG 10739/1–2 is difficult to determine because it is
427 fragmentary. The insertion area is covered by parallel to sub-parallel incomplete striae that
428 branch and converge in places and taper off both distally and proximally (Fig. 11D). There is
429 a c. 20^{o} angle between the striae and the IEB. The exsertion area is covered by tubercles,
430 which are arranged en échelon on the ornament ridges of NBMG 10739/1 and 4 (Fig. 11E),
431 and as near-straight ridges in NBMG 10739/2 and 5. The tubercles are elongated along the
432 long axis and intersect as even chevrons along the leading edge (Fig. 11C, E). The lengths of
433 the elongated tubercles vary from 400 to 910 μm in different spine fragments. Any
434 ornamentation originally present on the tubercles has been lost to abrasion. The angle between
435 the ornament ridges and the IEB varies from c. 81^{o} (Fig. 11B–C) in NBMG 10739/1–2 to c.
436 52^{o} in NBMG 10739/4 with the latter having more longitudinal elongate ridges to the long
437 axis, suggesting that it is part of the distal end of a pelvic spine (Turner *et al.* 2005). Spines
438 with varying levels of abrasion along their length may be indicative of wear during life
439 (Turner *et al.* 2005); if abrasion was caused by post-mortem transportation, then a more even
440 distribution of abrasion along the spine would be expected.

441 NBMG 10739/3–5, 7 and 10 are the only fragments complete enough for the cross-
442 sectional shape to be determined; all are elliptical (Fig. 11F). Only a single ridge is visible on
443 the trailing edge of NBMG 10739/3, as the surface is damaged where a second ridge would be

444 expected in *Gyracanthides* (Turner *et al.* 2005). There is an infilled circular hollow in NBMG
445 10739/4 that narrows distally in proportion with the narrowing of the spine. This hollow
446 represents the pulp cavity. All spine fragments are too small to show any distal curvature.
447 *Remarks.* Gyracanthid material from the Minto Formation has been reported previously as
448 *Gyracanthus* cf. *G. duplicatus* (Gardiner 1966; Miller 1999), but since Dawson's *Gyracanthus*
449 *duplicatus* is now known to be invalid (Carpenter *et al.* 2015), the Minto material merits re-
450 classification. Specimens NBMG 10736, NBMG 15173, NBMG 15826, NBMG 10739/1–11,
451 NBMG 19969 and NBMG 19970 have been removed from the genus *Gyracanthus* based on
452 having spines with ellipsoid cross sections, open grooved hollows and ornament ridges
453 showing a change in angle from oblique to parallel along the long axis of the pectoral spines.
454 These features are not characteristic of *Gyracanthus*, the spines of which have circular cross
455 sections and ornament ridges that are consistently oblique, but are characteristic of
456 *Gyracanthides* (Turner *et al.* 2005; Snyder 2011), to which we assign our specimens. Species-
457 level classification of *Gyracanthides* is based on tubercle orientation, ornamentation and
458 arrangement along the ornament ridges (Warren *et al.* 2000; Turner *et al.* 2005). As NBMG
459 15173 is highly abraded, this specimen cannot be assigned to a species. NBMG 10739/1 and
460 NBMG 10739/2 (Fig. 11B–C) show a much lesser degree of abrasion, yet no striae on the
461 tubercles can be seen, as in *Gyracanthides murrayi* (Warren *et al.* 2000, fig. 8e–f), indicating
462 that these spines still underwent a small degree of abrasion. The en échelon packaging of
463 tubercles on the ornament ridges better fits *Gyracanthides hawkinsi* than the straight ornament
464 ridges of *G. murrayi*, but ornamented ridges in *G. hawkinsi* meet along the leading edge in
465 uneven chevrons, which is not seen in specimen NBMG 10739/1–11, and tubercles have three
466 projections which converge towards the apex, again not seen in this specimen. Therefore we
467 assign all specimens to *Gyracanthides* sp.

468 Order ACANTHODIDA Berg, 1940

469 Family ACANTHODIDAE Huxley, 1861

470 Genus *ACANTHODES* Agassiz, 1843*b*

471 *Type species*. *Acanthodes bronni* Agassiz, 1843*b*

472 *Acanthodes* sp.

473 Figure 11G–H

474 *Material.* Four isolated spines (NBMG 15174, 15852, 15869, 15913).

475 *Diagnosis.* Slender, gently curving spines with a rounded anterior rib; lateral surfaces smooth
476 except for a single longitudinal groove on each side.

477 *Description.* Isolated, incomplete spines 10 to 32.5 mm in length and 0.5 to 2.5 mm wide,
478 exposed in lateral view. A rounded rib runs along the anterior surface, and is flanked on each
479 side by a prominent longitudinal groove; this is visible as an external mould in the matrix
480 where parts of the spine have been lost, confirming its presence on both sides. The spines are
481 otherwise smooth.

482 *Remarks.* The Acanthodidae were a highly cosmopolitan mid to late Palaeozoic group,
483 representatives of which have been found on every continent except South America (Denison
484 1979; Long 1986; Burrow *et al*. 2008; Sallan and Coates 2010). First appearing in the Middle
485 Devonian, this was the only acanthodiform family to persist into the Carboniferous and
486 Permian (Beznosov 2009; Sallan and Coates 2010). The best known acanthodidid genus,
487 *Acanthodes*, was widely distributed, occurring in Australia, South Africa, Europe, North
488 America, Greenland, and Siberia from the Middle Devonian to the late Permian (Denison
489 1979; Sallan and Coates 2010). However, the earliest known articulated specimens
490 (*Acanthodes lopatini* Rohon, 1889) are from the Tournaisian of south-central Siberia
491 (Beznosov 2009) and many earlier isolated scales and ichthyoliths assigned to *Acanthodes* sp.
492 are considered doubtful (Burrow *et al*. 2010).

493 Though other acanthodiforms were common in the Maritimes Basin of eastern Canada
494 during the Devonian (Gardiner 1966; Denison 1979; Kennedy *et al*. 2012), the only
495 previously reported occurrence of Acanthodidae is from the Tournaisian Horton Bluff
496 Formation of Nova Scotia (Zidek 1977; Mansky and Lucas 2013, fig. 13A), identified as
497 Acanthodidae indet. Thus, the four isolated spines (NBMG 15174, 15852, 15869, 15913),
498 reported here, are the first Canadian example of *Acanthodes* and extend the known range of
499 the Acanthodidae in Canada by some 35 million years. The acanthodid remains in the Horton
500 Bluff Formation are tantalising, because if they are in fact referable to *Acanthodes* this would
501 indicate a substantial ghost lineage, and suggest the lack of specimens from this interval is the
502 result of collection failure or taphonomic bias; it is to be hoped that further investigations in
503 the Horton Bluff Formation will provide determinable material which will resolve this issue.

504 Acanthodidae indet.

505 *Material*. Ten specimens containing multiple isolated spines (NBMG 15822, 15835, 15838,
506 15844, 15873, 16082, 16094, 16095, 20013, 20016).

507 *Diagnosis*. Slender, gently curving spines, unornamented except for a single prominent
508 longitudinal groove.

509 *Description*. Isolated, incomplete spines 5 to 25 mm long and 0.5 to 1.75 mm wide, exposed
510 in various aspects. Several have been crushed and badly damaged, so no further diagnostic
511 features can be discerned.

512

513 Class OSTEICHTHYES Huxley, 1880

514 Subclass SARCOPTERYGII Romer, 1955

515 Infraclass DIPNOMORPHA Ahlberg, 1991

516 Order DIPNOI Müller, 1845

517 Family *incertae sedis*

518 Genus *CTENODUS* Agassiz, 1843*a*

519 *Type species. Ctenodus cristatus* Agassiz, 1843*a*

520 *Ctenodus interruptus* Barkas, 1869

521 Figure 12A–B

522 *Material.* Two incomplete tooth-plates (NBMG 10740, 15822).

523 *Diagnosis*. Subtriangular tooth-plate with ridges that are near-parallel to one another. The
524 ridges are equipped with prominent, longitudinally compressed teeth with rounded apices.
525 *Description*. NBMG 10740 is a broken fragment of a tooth-plate. Only four near-parallel
526 ridges are present (Fig. 12A) with lengths of 9 to 31 mm, but these measurements do not
527 represent the original length of the ridges, as they are broken at both ends. There is a space of
528 5 mm between ridges (measured from between the apices). Individual apex height reduces
529 along each ridge from the centre out in both directions. Ridges are relatively straight. There is
530 a prominent depression between two apices on one side of the specimen (Fig. 12A), seen in
531 three of the ridges (not observable in the fourth ridge as this section of the ridge is not
532 preserved). Apices vary randomly along the ridge between conical and rounded (Fig. 12A);
533 rounded apices are likely a result of abrasion. All apices are laterally compressed towards the
534 apex. The basal surface is encased in sediment.
535 *Remarks.* Only two species of *Ctenodus* have been reported from the North American
536 continent: *C. cristatus* and *C. interruptus*, with *C. murchisoni* from Nova Scotia being
537 assigned to *Conchodus plicatus* (Baird 1978). NBMG 10740 shows more prominent separated
538 apices than *C. cristatus* (Sharp and Clack 2013, fig. 2) and *C. murchisoni* (Sternberg 1941,
539 fig. 1–3). These prominent apices are similar to *C. interruptus* (see Sharp and Clack 2013, fig.
540 5, 14). Therefore NBMG 10740 has been assigned to *C. interruptus*. Ahlberg *et al.* (2006), in
541 their review of the development of lungfish dentitions, convincingly argue that these apices

542 are teeth and not denticles, as described in older literature. The dental plate bears some very
543 small xenacanthid teeth on the occlusal surfaces (Fig. 12B).

544 Dipnoi indet.

545 Figure 12C–D

546 *Material*. Six specimens, each comprising isolated tooth-plate fragments (NBMG 18609,
547 19698–19701, 19833).

548 *Diagnosis.* Triangular tooth-plates equipped with ridges of teeth.

549 *Description.* Fragmentary tooth-plates, each bearing two ridges, converging at an angle of c.
550 20° (Fig. 12C). There is no evidence that any other ridges were originally present. Teeth are
551 laterally compressed, and this is consistently more pronounced in one ridge than the other
552 (Fig. 12D). Tooth-plates show broken surfaces near the edges.

553 *Remarks*. Dipnoan tooth-plates show substantial variation attributed to tooth wear (Schultze
554 and Chorn 1997) and to developmental anomalies (Kemp 1996, 2003), making the
555 identification of isolated specimens difficult. Most diagnostic characters are associated with
556 cranial bones rather than tooth-plates (Sharp and Clack 2013), although isolated tooth-plates
557 can often be identified to species level when complete (Sharp and Clack 2013). Due to the
558 fragmentary nature of the specimens they have been assigned to Dipnoi indet.

559

560 Infraclass TETRAPODOMORPHA Ahlberg, 1991

561 Order RHIZODONTIDA Andrews and Westoll, 1970 emend. Johanson and Ahlberg, 2001

562 Family RHIZODONTIDAE Traquair, 1881*a* emend. Andrews and Westoll, 1970

563 Genus *STREPSODUS* Huxley, *in* Huxley and Etheridge, 1865

564 *Type species. Strepsodus sauroides* Binney, 1841

565 *Strepsodus sauroides* Binney, 1841

566 Figure 13A

567 *Material.* Nine isolated teeth (NBMG 9969, 15005, 15007, 15788, 15815, 15820, 15829–
568 15830, 19688).
569 *Diagnosis.* Tall, slender teeth that are recurved lingually. Teeth are oval in cross section.
570 Reversed curvature is present towards the apex of the crown. Raised parallel striae are present
571 on the lingual side and on the lingual portions of the distal and mesial sides of the teeth. Striae
572 are longitudinal and show minor to no degree of curvature.
573 *Description*. Incomplete teeth varying in length from 7 mm in NBMG 9969 to 17 mm in
574 NBMG 15820. Teeth have an oval cross section. Teeth are recurved and show reverse-
575 curvature near the apex (Fig. 13A), giving them a sigmoidal shape. Raised striae are
576 longitudinal and some show minor curvature, particularly towards the apex, causing
577 individual striae to cross from the lingual surface to the mesial/distal sides. Striae subside near
578 the apex and are absent on the apex itself. Striae may appear to converge apically as a result of
579 recurvature, yet they never come into direct contact. Instead a stria caught between two
580 converging striae will taper out. Striae show a maximum spacing of 0.1 mm prior to
581 convergence. This distance is consistent irrespective of tooth size; larger teeth simply bear
582 more striae. The base of the crown is absent in all specimens.
583 *Remarks*. Reverse curvature seen in NBMG 9969 and possibly present in NBMG 15820
584 suggests that these may be symphysial tusks, but the small size of NBMG 9969 and the lack
585 of well-preserved *Strepsodus* mandibles makes this uncertain (Jeffery 2003, 2006).
586 Genus *ARCHICHTHYS* Hancock and Atthey, 1870
587 *Type species. Archichthys portlocki* Portlock, 1843 ex Agassiz MS
588 *Archichthys portlocki* Portlock, 1843 ex Agassiz MS
589 Figure 13B–C
590 *Material.* Three isolated teeth (NBMG 15799, 15818, 19972).

Diagnosis. Robust, gently curved teeth with 11 plications around the base. A 'woven' pattern of striation is present above the plications.

Description. NBMG 19972 is a robust tooth 14 mm long. Teeth show gentle lingual curvature (Fig. 13B) with an oval cross section, and are equipped with 11 basal plications (Fig. 13C). Striations on the exposed parts of the tooth surface form a "woven" texture; these are most pronounced at the base of the teeth, and become fainter apically, disappearing completely at the apex. Although the labial surface of NBMG 19972 is partially covered in sediment, an exposed part lacks striations.

Remarks. The 11 plications reported from NBMG 19972 are fewer than the 16 to 18 recorded by Jeffery (2006). This does not rule out assigning NBMG 19972 to *Archichthys portlocki*, as the plication count did not form part of the diagnosis of the species by Jeffery (2006). A plication count of 11 agrees with the estimated 10 to 12 for *A. portlocki* in Carpenter *et al.* (2015). Although the striations in NBMG 15799, NBMG 15818 and NBMG 19972 are similar to those of *Letognathus* (Brazeau 2005), this assignment has been ruled out because, unlike *Letognathus*, striations are absent from the labial surface of all three teeth, as expected for *A. portlocki* (Jeffery 2006). The teeth of *Letognathus* are long and slender (Brazeau 2005), unlike the robust teeth of NBMG 15799, NBMG 15818 and NBMG 19972, again supporting our identification.

cf. *Archichthys portlocki* Portlock, 1843 ex Agassiz MS

Figure 13D–E

Material. Two isolated scales (NBMG 15831, 19689).

Diagnosis. Sub-hexagonal scales with concentric growth lines becoming more prominent towards the periphery of the scale. Median boss on the inner surface.

Description. Two incomplete sub-hexagonal scales with the inner surface exposed. NBMG 19689 has a diameter of 25 mm (Fig. 13D) and NBMG 15831 has a length of 16 mm and a

width of 24 mm (Fig. 13E). Concentric growth rings are most prominent at the periphery of the scale and diminish towards the centre. NBMG 19689 has an elongated median boss 4 mm long and 2 mm wide. NBMG 15831 has a pentagon-shaped median boss 1 mm across.

Remarks. NBMG 15831 and NBMG 19689 resemble scales, which formed part of the type series for *Archichthys portlocki* (Portlock 1843, reproduced in Jeffery 2006, fig. 1). Surface detail is partially obscured by a light coating of very fine sediment which proved impossible to remove without damaging the scale.

Genus *RHIZODUS* Owen, 1840

Type species. Rhizodus hibberti Owen, 1840

Rhizodontidae cf. *Rhizodus hibberti* Owen, 1840

Figure 13F

Material. 15 specimens comprising isolated tusks (NBMG 15787, 15789-15791, 15795, 15798, 15809-15810, 15812-15813, 15816-15817, 15862, 15866, 16074).

Diagnosis. Large tusks with lenticulate cross-section. Approximately 24 plications.

Description. NBMG 15809 is a single robust tusk partially covered in matrix. The exposed portion is 29 mm long. The apex of the crown is either covered in matrix or absent. The exposed surface of the base of the crown is equipped with 12 plications. Recurvature, if any, cannot be observed due to matrix cover. The tusk is slightly compressed which has resulted in longitudinal fractures.

Remarks. Based on the number of plications (n = 12) visible on the exposed portion of NBMG 15809, it is likely that the tooth bears 22 to 26 in total. Similar tusk morphotypes from different genera of rhizodont are differentiated based on the number of plications (Jeffery 2003). This tusk cannot be *Archichthys portlocki* or *Letognathus hardingi* because they bear 16 to 18 and around 14 plications, respectively (Brazeau 2005; Jeffery 2006). *Strepsodus sauroides* is also excluded because it lacks striations. An estimated plication count of 22 to 26

641 is consistent with *Rhizodus hibberti* (20 to 22) and *Barameda decipiens* (20 to 26) (Jeffery
642 2003; Holland *et al.* 2007). As *B. decipiens* is known mostly from Australia, whilst *R. hibberti*
643 is found in North American and European localities, this is more likely *R. hibberti*. Isolated
644 tusks of *R. hibberti* and *Screbinodus ornatus* are only distinguishable based on size (Jeffery
645 2003); with a minimum crown height of 26 mm, we assign NBMG 15809 to Rhizodontidae
646 cf. *Rhizodus hibberti*.

647 Order *incertae sedis*Family MEGALICHTHYIDAE Hay, 1902

648 Genus *RHIZODOPSIS* Young, 1866 ex Huxley MS emend. Traquair, 1881*b*

649 *Type species. Rhizodopsis sauroides* Williamson, 1849

650 Tetrapodomorpha indet., cf. *Rhizodopsis sauroides* Williamson, 1849

651 Figure 13G

652 *Material*. One specimen comprising a single isolated scale (NBMG 15901).

653 *Diagnosis.* Ovoid scale, divided into four quadrants. Concentric growth lines present in all
654 quadrants. Radial striae present in only the posterior and anterior quadrants. A median boss
655 and concentric growth lines are present on the inner surface.

656 *Description.* Elongated ovoid scale with a length of 26.5 mm and a maximum width of 14
657 mm. The scale is embedded in the matrix with the inner surface exposed. The scale is
658 fractured, but almost complete, with only a small section of the outer edge broken off (Fig.
659 13G). Quadrants can be identified, but with great difficulty, and concentric growth lines can
660 be seen only along the very edges. Radial striae can be seen in parts only along the outer edge.
661 There is a median boss on the inner surface, elongated along the long axis. The median boss is
662 4 mm long and 1 mm thick. The scale is marked by punctae, 400 μm in diameter.

663 *Remarks*. The placement of *Rhizodopsis* as a sister-taxon to *Megalichthys* (Friedman *et al*.
664 2007) has led to its transferal from Rhizodopsidae Berg (1940) to Megalichthyidae Hay
665 (1902) and thus it has been referred to as a megalichthyid (Coates *et al*. 2008). Detail on the

surface of NBMG 15901 has been lost, seen in the lack of concentric growth lines towards the centre of the scale, making identification uncertain. Overall scale morphology looks similar to that illustrated by Williamson (1837, fig. 1, 4), with NMBG 15901 being slightly more ovoid. This less rhombic morphology is seen in other *Rhizodopsis sauroides* scales (e.g. Holland *et al*. 2010, fig 6f reproduced from Woodward 1891). The median boss of NBMG 15901 resembles the median boss illustrated by Williamson (1837, fig. 1, 4). *Megalichthys* scales with the cosmine removed have been misidentified as the scales of *Rhizodopsis* (Holland *et al*. 2010), but as the scales of *Megalichthys* lack a median boss (Andrew and Westoll 1970) it is certain that NBMG 15901 does not belong to *Megalichthys*. For the present, NBMG 15901 is placed in Tetrapodomorpha indet. cf. *Rhizodopsis sauroides*.

Order Sarcopterygii *incertae sedis*

Family MEGALICHTHYIDAE Hay, 1902

Genus *MEGALICHTHYS* Agassiz, 1843*b*

Type species. *Megalichthys hibberti* Agassiz, 1843*b*

Megalichthys sp.

Figure 13H–J

Material. Four specimens (NBMG 10741 in two parts, 15794, 19974). One of these blocks contains up to 11 identifiable fragmented scales (NBMG 10741/1) and seven complete scales in the other part (NBMG 10741/2–7).

Diagnosis. Sub-rhombic scales with a cosmine-covered outer surface.

Description. Fractured rhombic scales c. 25 mm in length where complete (Fig. 13H). Cosmine-covered outer surface with very low relief ripple-like ornamentation (Fig. 13I). There is a cosmine-free ridge at the margin of the cosmine-covered outer surface, which gradually thins towards the outer edge of the scale. Where the cosmine covering has been worn away from the scales, the surface is covered by closely spaced punctae. On the inner

surface is a prominent ridge, which follows the line of contact between the cosmine-covered portion and the ridge on the free field. The ridge on the inner surface does not extend to the margins and tapers off sharply in a stepwise fashion (Fig. 13J). This gives the ridge an elongated rectangular shape.

Remarks. Genus- and species-level identification of megalichthyids is based on cranial characters (Thompson 1964; Andrews 1985, Fox *et al*. 1995), but as *Megalichthys* is common throughout the Carboniferous Maritime Basin it is reasonable to associate these rhombic scales with the genus (e.g., Carpenter *et al.* 2015).

cf. *Megalichthys* sp.

Figure 13K–L

Material. One specimen, a single isolated centrum (NBMG 19958).

Diagnosis. Annular centrum with a relatively large notochordal canal.

Description. NBMG 19958 is a single annular centrum with an outer diameter of 27 mm (Fig. 13K) and a thickness of 5.5 mm (Fig. 13L). The inner surface tapers to form a ridge-like structure, and a relatively large notochordal canal (diameter 16 mm) is inferred. Therefore the inner/outer diameter ratio is 1.69. The inner and outer surface is rough and has a worn appearance. There is no evidence of a neural arch or spine.

Remarks. The worn texture of the centrum suggests that smooth or wrinkled periosteal bone is absent, which may be the reason why triangular areas over the posteroventral regions are absent (see Andrews and Westoll 1970, fig. 7d). The inner/outer diameter ratio of NBMG 19958 is slightly larger than the typical ratio seen in *Megalichthys hibberti*, but ratios in excess of 1.6 have been noted (Andrews and Westoll 1970). Based on its size, this centrum would have been from the trunk of the fish. Neural arches are present in some, but not all, megalichthyid trunk vertebrae, meaning that the lack of a neural arch does not exclude this specimen from the trunk (Andrews and Westoll 1970). The higher outer/inner diameter ratio

716 of NBMG 19958 compared to *Megalichthys hibberti*, along with the difficulty of assigning a
717 single isolated worn centrum to a species, means we assign it to cf. *Megalichthys* sp.

718 Tetrapodomorpha indet.

719 Figure 13M–N

720 *Material.* Thirteen specimens, comprising incomplete, isolated teeth (NBMG 9968, 10776,
721 10777, 10783, 10785, 19691-19697) and scales (NBMG 20014)

722 *Diagnosis.* Recurved conical teeth with a smooth surface, lacking cutting edges.

723 *Description.* The teeth are conical teeth and very gently curved (Fig. 13M); however, NBMG
724 10785 [figure reference here?] has been flattened to such a degree that it is impossible to tell if
725 the tooth was ever recurved. NBMG 19696 has a circular cross section exposing a sediment-
726 filled pulp cavity. NBMG 10777 (Fig. 13N) has a broken side exposing part of the pulp cavity
727 that has likewise been filled with sediment. The crown base is absent in all specimens.

728 *Remarks*. Apical caps lacking acrodin exclude these teeth from Actinopterygii, so they are
729 identified as sarcopterygians. Sediment-filled pulp cavities suggest that NBMG 19696 and
730 NBMG 10777 had hollow pulp cavities, which are indicative of polyplocodont teeth, such as
731 are present in *Megalichthys*, *Rhizodopsis*, *Rhizodus* and *Strepsodus* (Schultze 1970).
732 Polyplocodont teeth are also present in primitive crown tetrapods, so a tetrapod affinity cannot
733 be ruled out. Without further histological investigation and in the absence of a tooth base,
734 plication folding cannot be determined and these teeth cannot be identified more precisely
735 (Schultz 1970; Vorobyeva 1977; Jeffery 2003). Therefore we identify these teeth as
736 Tetrapodomopha indet.

737

738 Superclass TETRAPODA Goodrich, 1930

739 Figure 14–D

740 *Material.* Fifteen specimens, including partial jaws (NBMG 15821, 15853, 15872, 20019,
741 20020, 20021), dermal cranial bones (NBMG 15785, 20028), vertebrae (NBMG 15783,
742 15784, 15870), ribs (NBMG 15782, 15914), possible limb bones (NBMG 15915).
743
744 *Description.* NBMG 15821 is the most complete of several jaw bones; it comprises a 14 mm
745 long mandible, with at least 17 elongate, straight, bullet-shaped, pointed teeth that bear faint
746 longitudinal striations confined to the basal one-third of the visible portion of the crown (Fig.
747 14A). The jaw bone, although somewhat damaged, appears to be narrow, barely as deep as
748 the length of the tooth crowns, and it bears a shallow sculpture of longitudinal ridges. NMBG
749 15783 is a vertebra comprising a disc-shaped inter- or pleurocentrum, with nearly
750 equidimensional measurements in articular view (Fig. 14B), and anteroposteriorly short (Fig.
751 14C), and with a central notochordal canal. In lateral view (Fig. 14C), the portion of the
752 lateral surface between the projecting, rolled edges around the articular faces is depressed.
753 NBMG 15915 is one of several small limb bones (Fig. 14D); it is 19 mm long, shows
754 expanded articular ends, 5 mm across, and a narrow shaft, 2 mm wide at its narrowest. The
755 expansions are more or less symmetrical at each end, forming a roller structure at the left-
756 hand end and a shallow socket at the right-hand end, as illustrated. These are the
757 characteristics of a phalangeal bone from the hand or foot. Because of its relative length, this
758 could be the phalanx from one of the longer toes of the foot of an early tetrapod.
759 DESCRIBE RIBS AND CRANIAL BONES?
760 *Remarks.* Material includes several small jaw bones, cranial bones, vertebra, ribs, and limb
761 bones that do not appear to correspond to any of the fishes described above, but more closely
762 resemble those of tetrapods. Jaw material shows similarities to those of stem tetrapods
763 (colosteids) and anthracosaurs (embolomeres) (Carroll 2009); however, neither of these
764 groups of tetrapods have maxillaries or dentary rows with diagnostic features that would

765 allow attribution with confidence (Bolt and Lombard 2010). The vertebral centrum (NMBG
766 15783) is reminiscent of those of embolomerous anthracosaurs (e.g. 'rolled up' projections of
767 the peripheral margins of its anterior and posterior surfaces; markedly arcuate dorsal and
768 ventral profile of vertebral body in lateral view); however, some lungfish have similar disc-
769 shaped centra (e.g. *Griphoganthus* from the Devonian of Australia; Campbell & Barwick
770 2002) so a dipnoan affinity cannot be entirely discounted. These preliminary remarks do not
771 allow us to make confident interpretations of the tetrapod fauna.
772
773 Subclass ACTINOPTERYGII Cope, 1887
774 Order EURYNOTIFORMES Sallan and Coates, 2013
775 EURYNOTIFORMES indet.
776 Fig. 15A
777 *Material*. Incomplete mandible with five attached teeth (NBMG 20021).
778 *Diagnosis*. Teeth smooth, bulbous and conical, with apical caps of acrodin.
779 *Description*. Isolated mandibular fragment c. 2 mm in length. The teeth are bulbous, conical,
780 and unornamented; they are also very small, measuring only c. 0.75 mm.
781 *Remarks*. Durophagous actinopterygians first appeared during the Tournaisian (Sallan and
782 Coates 2010), and are believed to have undergone at least two significant radiations in
783 Euramerica during the Carboniferous; hence, they are a common component of Pennsylvanian
784 fossil assemblages in North America and Europe (Zidek 1992; Mickle and Bader 2009; Sallan
785 and Coates 2010). Although their systematic status is yet to be fully resolved, most genera can
786 be placed into either Eurynotiformes Sallan and Coates, 2013 or the likely paraphyletic
787 Bobasatraniiformes Berg, 1940 (Mickle and Bader 2009; Sallan and Coates 2013). The
788 Eurynotiformes possessed a heterognathic dentition consisting of phyllodont tooth plates and
789 a denticulated maxilla; anterior maxilliary teeth were tall and conical, while posterior teeth

were much more tumid (Sallan and Coates 2013, fig. 14b). In contrast, the Bobasatraniiformes were equipped with similar tooth plates (Johnson and Zidek 1981; Zidek 1992) but otherwise appear to have been generally edentulous (Campbell and Le Duy Phuoc 1983; Zidek 1992; Mickle and Bader 2009).

Three eurynotiform genera (*Eurynotus*, *Mesolepis*, and *Amphicentrum*) are known to have persisted into the Pennsylvanian (Sallan and Coates 2013), but isolated teeth of these taxa cannot be distinguished from one another.

Actinopterygii indet.

Figure 15B–E

Material. Eight specimens containing 25 isolated scales (NBMG 18608, 19678–19683, 20015), ten specimens containing 172 cranial bone fragments (NBMG 19799–19808), one isolated tooth (NBMG 19684), and four isolated centra (NBMG 19834, 19685–19687).

Diagnosis. Rhombic scales with a covering of ganoine, peg-and-socket articulation and asymmetrical serrations. Disc shaped cranial bone fragments with elongated ridges on the outer surface. Conical teeth with a distinct apical cap. Hour-glass shaped centra with concave depressions.

Description. Scales: Rhombic scales 0.5 to 1 mm in size. Four scales have asymmetrical serrations on the posterior margin (Fig. 15B–C). Dorsal and ventral margins are straight with slight curvature near the anterior and posterior margins. The anterior margins are slightly curved along their entire extent. Sockets from peg-and-socket articulation are present in seven of the scales (Fig. 15C). *Cranial Bone Fragments:* Elongated sub-rectangular shaped bone plates with a maximum long axis of 2.5 mm. NBMG 19804 has closely packed, branching ridges present on the outer surface (Fig. 15D), which vary along the surface from longitudinal to curved. The inner surface is smooth lacking a peg-and-socket articulation. *Tooth:* NBMG 19684 is a slender, recurved conical tooth with translucent apical cap (Fig. 15E). *Centra:*

NBMG 19686 measures 1.22 mm from anterior to posterior margin and 0.5 mm in maximum height, giving a height:length ratio of 2.44. The centrum becomes constricted towards the centre (Fig. 15F) producing an 'hour glass-shape' (Schultz and Chorn 1986). Concave posterior and anterior margins form 'cup' shapes on either end that are infilled with sediment. On the dorsal surface there are two sockets elongated along the long axis and separated by a trough. These sockets would have housed the neural arches. A rounded attachment site is present only on one of the lateral sides, which extends laterally (Fig. 15F). On the other lateral side it is likely that an attachment site was present, but has been broken off. A thin ridge runs along the long axis of the ventral surface.

Remarks. The interrelationships of basal Actinopterygii are poorly understood (Patterson 1982; Gardiner 1984; Gardiner and Schaeffer 1989; Sallan 2014), and certain groups, such as the Palaeonisciformes, are certainly paraphyletic (Janvier 1996), making the placement of ichthyoliths in mid-level taxonomic groups problematic. Peg-and-socket articulation in NBMG 19679/1 is similar to that depicted by Schultze (1966, fig. 1a–b) and was previously thought characteristic of ganoid fishes, but the discovery of cladistian scales with peg-and-socket articulation suggests that it is plesiomorphic within the Actinopterygii (Schultze 1977; Patterson 1982). The ridge patterns on the cranial bone fragments, from the Minto specimen, resemble to a limited degree the pattern of ridges seen in the rostral and premaxilla of *Gogosardia coatesi* illustrated in Choo *et al*. (2009, fig. 8a-b) suggesting they are of palaeoniscoid-type. Wide variation in the ridges of cranial bones (Choo *et al.* 2009; Choo 2011, 2015) means that identification of fragmented cranial bones is problematic. Likewise, the high variability of scale morphologies in early Actinopterygii means that it is difficult to say whether the Minto Formation scales represent one or more species (Choo 2011). The apical cap of NBMG 19684 is composed of modified dentine called acrodin (Ørvig 1978), found only in the teeth of Actinopterygii, including cladistians, some palaeonisciformes,

colobodonts and pycnodonts (Ørvig 1978; Patterson 1982), though it is absent in pachycormids, *Cheirolepis* and *Severnichthys* (Patterson 1982; Carpenter *et al*. 2014). The centra resemble those of palaeoniscoids illustrated by Schultz and Chorn (1986, fig 3.1–2). The presence of lateral attachment sites, which would have served as attachment points for the ribs, and a height:length ratio of 1:2.44 suggests that these centra formed part of the abdominal region (Schultz and Chorn 1986), although this is higher than a ratio of 1:1.5 recorded by Schultz and Chorn (1986).

BROMALITES

Heteropolar microspiral coprolites

Figure 16A–B, E

Material. Thirty-three specimens (NBMG 18789, 19975–19998, 20004–20011).

Diagnosis. Spiral coprolites, with coils concentrated at the posterior end, covering < 50% of the total length, and striae parallel to the long-axis at the anterior end.

Description. Spiral coprolites, dark grey to brown in colour, 12 to 37 mm long and 5 to 14 mm in diameter (Fig. 16A). Coprolites characterised by six to 12 coils, typically 1 to 2.5 mm wide, concentrated at the posterior end, and comprising up to 50% of the total length (Coprolite Type F3 of Hunt and Lucas 2012*a*). The anterior end is characterised by prominent striae, parallel to the long axis, but twisted into a corkscrew. In thin section, posterior coils are recognisable (Fig. 16B), and the bulk of the coprolites comprise amorphous to pelleted phosphatic grains. Abundant fish skeletal material is also present including recognisable bicupsid xenacantid teeth, although their very small size could indicate an origin in a juvenile shark (Fig. 16E).

Remarks. Heteropolar spiral coprolites were produced by fishes with valvular intestines (McAllister 1987), and represent fully evacuated coprolites rather than enterolites preserved *in*

865 *situ* (Hunt *et al.* 2012; Hunt and Lucas 2012*a, b*). The phylogenetic distribution of this
866 intestinal structure is not well understood, but it is generally considered to be a primitive
867 feature, most characteristic of elasmobranchs; it is absent in more derived fishes such as
868 actinopterygians and teleosts (Hunt and Lucas 2012*a*). Various authors have argued that
869 xenacanthiform sharks were the most likely producers of spiral coprolites in the
870 Pennsylvanian-Permian of U.S.A. (Williams 1972; McAllister 1985; Hampe 1988). Johnson
871 (1999) and Hunt *et al.* (2012) described similar coprolites to those reported here from the
872 Pennsylvanian-Permian of U.S.A. and related them to *Orthacanthus* sharks, in particular,
873 based on quantitative co-occurrence data. Given the large size of our coprolites and the
874 abundance of *Orthacanthus* teeth in the Coal Creek assemblages where the heteropolar
875 coprolites co-occur, a biological association is considered very likely. Based on the
876 occurrence of small xenacanthid teeth within the coprolite, *Orthacanthus* may have fed on
877 juvenile sharks amongst other prey.

878 Short cylindrical coprolites

879 Figure 16C–D

880 *Material.* Four specimens (NBMG 19999–20002).

881 *Diagnosis.* Short cylindrical coprolites with the posterior end rounded, and the anterior end
882 slightly to strongly tapered.

883 *Description*. Light grey, calcareous coprolites, comprising a short cylindrical morphology
884 with two rounded ends or an anterior taper resulting in a tear-drop shape (Coprolite Types B1
885 and B2 of Hunt and Lucas 2012*a*). Coprolites are 20 to 60 mm long and 6 to 20 mm in
886 diameter, and comprise a dense, solid posterior mass and a more diffuse anterior zone (Fig.
887 16D). Invertebrate fragments, < 1 mm in granularity, are abundant, especially at the anterior
888 end and include recognisable microconchids and bivalve fragments, possibly of *Naiadites* type
889 (Fig. 16C).

Remarks. The calcareous composition, and the presence of recognisable shelly fragments, indicates that the producer fed on invertebrates. The producer cannot be identified but the crushed shelly components suggest a durophagous habit facilitated by grinding tooth plates, most consistent with the lungfish *Ctenodus*. The size of the coprolite suggests that the fish that produced it was relatively large.

Subspherical coprolite

Figure 16F–G

Material. One specimen (NBMG 19824).

Diagnosis. Short coprolite, approximately as wide as tall, rounded in all dimensions, showing a bilobed external appearance.

Description. The specimen is somewhat nondescript, and can simply be termed 'round', or as a subrounded small pellet (category C1), using the shape scheme of Hunt and Lucas (2012*a*, *b*). The coprolite is bilobed, with two equal-sized subspherical portions largely overlapping, and presumably reflecting the original structure. It measures 19 x 22 mm, and is, at most, 7 mm thick. The thickness is probably reduced by compaction and by breakage; one side appears to be external, the other internal (Fig. 16F), showing numerous broken pieces of bone, scales, and teeth preserved. These fish skeletal fragments (Fig. 16G) include a portion of a ridged tooth, preserved shiny and black, possibly from a rhizodont, as well as unidentifiable portions of scales and bones.

Remarks. The coprolite is not especially distinctive; however, based on its size and its contents, it is assignable to a relatively large predatory animal, perhaps a xenacanth shark, rhizodont, or even an aquatic tetrapod.

DOMINANCE-DIVERSITY ANALYSIS

914 The taxonomic make-up of a total of 722 hand specimens, each containing at least one fish
915 fragment, was analysed quantitatively, at order/class and generic level, with indeterminate
916 material discarded (Table 2). At order/class level, the assemblage (n = 325 identifiable hand
917 specimens) is dominated by chondrichthyans (64.3%), with common sarcopterygians (17.8%)
918 and rare actinopterygians (8.0%), acanthodians (5.2%) and tetrapods (4.6%). At generic level
919 (n = 182 identifiable hand specimens), chondrichthyans are even more dominant with
920 *Ageleodus* (37.0%) and *Orthacanthus* (39.2%) comprising nearly four fifths of the
921 assemblage, while four sarcopterygians, *Rhizodus* (8.8%), *Strepsodus* (5.0%), *Megalichthys*
922 (2.8%), and *Archichthys* (2.8%) make up most of the rest of the total. Note that these figures
923 represent raw totals, based on the fossils, and they take no account of the differing biology of
924 the various taxa. In particular, the dominance by chondrichthyans may reflect, in part, the fact
925 that these taxa, presumably, shed teeth throughout their lives, as do modern elasmobranchs.
926 This would inflate the chondrichthyan sample by several multiples. There are no reliable
927 adjustment factors that can be used to relate fossil assemblage data to original fish population
928 pyramids.

929 In order to examine palaeoecological patterns, specimens were assigned to one of the
930 four sedimentary facies (Ó Gogáin *et al*. 2016, Supplementary Dataset 1) and analysed in a
931 palaeoenvironmental context: shallow marine facies (Lithology 1), brackish embayment facies
932 (Lithology 2), or brackish tidal estuary facies (Lithology 3 and 4). Fish and tetrapod remains
933 are considered parautochthonous to each facies in which they are found. This is based on the
934 fact that all material shows no signs of abrasion, with the exception of abrasion on the distal
935 portions of the spines of *Gyracanthides*, which is attributed to wear during life, suggesting
936 minimal transportation. However the possibility that fish and tetrapod remains washed in from
937 other environments cannot be entirely ruled out and the disarticulated nature of the material
938 indicates that there was at least some minimal washing.

939 We note that analysis of the facies distribution of fishes across this offshore to onshore
940 salinity gradient is hampered by the fact that three-quarters of determinate specimens derive
941 from the brackish embayment facies (Lithology 2) whereas fossils in the offshore shallow
942 marine facies (Lithology 1) and onshore tidal estuary facies (Lithology 3 and 4) are relatively
943 rare. Acknowledging this limitation, genus-level data was analysed using the inverse of the
944 Simpson Index given by the equation:

945 $$D = 1 - \left(\sum \frac{n(n-1)}{N(N-1)} \right),$$

946 where n is the total number of specimens of a particular genus and N is the total number of
947 specimens of all genera. This analysis shows that diversity, measured in terms of the total
948 number of taxa and the evenness of the abundance distributions of those taxa, is highest in the
949 shallow marine environment (D = 0.805) and progressively declines in the brackish
950 embayment (D = 0.641) and tidal estuary (D = 0.428). Examining these data qualitatively also
951 reveals patterns. It is noteworthy that both shark genera, *Ageleodus* and *Orthacanthus*, are
952 distributed across the salinity gradient (Lithology 1 – 4) in relatively high proportions. Here,
953 the equally high proportions of sharks across all facies may help mitigate biasing effects of
954 their relative over-abundance because of tooth shedding. In contrast, dipnoans (*Ctenodus*),
955 rhizodonts (*Archichthys*, *Strepsodus*) and *Megalichthys* occur in higher proportions in the
956 marine facies (Lithology 1) while some other rhizodonts (*Rhizodus*) and *Rhizodopsis* are more
957 common in brackish tidal estuaries.

958

959 **DISCUSSION**

960 In this paper, we document a new, diverse assemblage of fish and tetrapods in a facies context
961 from the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada.
962 Findings improve knowledge of the biodiversity, food webs, and ecology of fish and tetrapod
963 communities during a critical evolutionary phase.

964

965 *Biodiversity and food webs*

966 Based on specimen counts, the dominant fish were chondrichthyans, comprising 64.3% of the
967 assemblage based on class-level counts. As noted, this value is likely inflated by the common
968 shedding of teeth by sharks. Two genera are co-dominant. Most common (39.2%) is
969 *Orthacanthus*, a large predatory shark that reached its acme in Pennsylvanian times. The diet
970 of *Orthacanthus* was catholic, including actinopterygians, acanthodians, dipnoans,
971 xenacanthids, and tetrapods, based on analysis of coprolites (Williams 1972; Hampe 1988;
972 Johnson 1999) and gut contents (Kriwet *et al.* 2008). However, the presence of possible
973 juvenile xenacanthid remains in heteropolar microspiral coprolites, reported here, adds
974 another dimension to our understanding of *Orthacanthus* behaviour. It suggests the genus was
975 practising filial cannibalism of juvenile xenacanthids (as postulated at other sites; Hampe
976 1988; Soler-Gijon 1995; Heidke 1998; Johnson 1999; Beck *et al.* 2014). The ecology of the
977 other abundant shark, *Ageleodus*, remains completely unknown, and it is even uncertain
978 whether skeletal elements represent teeth or specialised branchial denticles (Lebedev 1996;
979 Turner 2013).

980 The assemblage, also, contains common (17.8%) sarcopterygians (rhizodontids,
981 megalichthyids, rhizodopsids) and rare aquatic tetrapods (4.6%), which were similar large
982 predatory animals. Subspherical coprolites containing rhizodont and actinopterygian remains
983 may have been derived from either of these groups. The dominance of large predators
984 (secondary and tertiary consumers) is inconsistent with a normal trophic pyramid. However,
985 this inverted structure is commonly reported for Pennsylvanian assemblages (e.g. Carpenter *et*
986 *al.* 2015), and may simply reflect a much lower preservation potential of, mostly soft-bodied,
987 producers and primary consumers.

Within the fish assemblage, the acanthodians (5.2%) had differing feeding habitats. *Acanthodes* was likely a suspension feeder (Brazeau and Winter 2015) filtering planktonic organisms, while *Gyracanthides*, which based upon abrasion on pelvic and pectoral spines (Denison 1979) occupied a partial benthic habitat and possibly feed on small benthos. Also present were eurynotiforms and the dipnoan, *Ctenodus*, whose crushing/grinding dentition suggests a durophagous mode of life. Based on their size, dipnoans were the most likely producer of the short ellipsoid coprolites that contain fragmentary invertebrate remains (microconchids, bivalves) and rare fish fragments. Non-eurynotiform actinopterygians may have fed on a variety of organisms including zooplankton, arthropods or other fish but due to the fragmentary nature of the associated material this cannot be deduced with any certainty.

Euryhaline tolerances

The fish and tetrapod assemblages date from the early Moscovian acme of a major diversification event within brackish/freshwater environments (Falcon-Lang *et al.* 2015*a*). Acquisation of a euryhaline habitat within Carboniferous fish groups occurred prior to the diversification event (Sallan and Coates 2010, 2014; Friedman and Sallan 2012). However, there is considerable disagreement as to whether Carboniferous fish communities documented from continental facies were adapted for a euryhaline habitat. Some authors agree that fish communities were, indeed, temporary visitors from adjacent marine environments because their cosmopolitan distribution implies dispersal via marine seaways (Schultze 2009; Carpenter *et al.* 2011, 2014, 2015). In contrast, others have maintained that they comprised elements of an endemic freshwater ecosystem because the strontium isotope ratio ($^{87}Sr/^{86}Sr$) of apatite tooth enamel (0.70824 to 0.71216) suggests substantial contact with continental-influenced water bodies (Masson and Rust 1984; Śtamberg and Zajíc 2008; Fischer *et al.* 2011, 2013; Montañez and Cecil 2013).

Quantitative analysis of fish remains in a facies context, reported here, indicate that some fish taxa at least were euryhaline, but also reveals previously unsuspected ecological heterogeneity. Chondrichthyans appear to have been particularly successful in colonising the full salinity gradient, and both *Orthacanthus* and *Ageleodus* have been found in apparently freshwater fluviolacustrine facies upstream of the marine coast at other sites (Schneider *et al*. 2000; Hampe 2002; Carpenter *et al*. 2014). This is also the case for *Acanthodes*, which been reported from a variety of lacustrine, fluvial, estuarine/deltaic, and fully marine settings (Zidek 1976; Beznosov 2009; Burrow *et al*. 2010; Sallan and Coates 2010). In contrast, while also likely euryhaline, dipnoans (*Ctenodus*), rhizodonts (*Archichthys*, *Strepsodus*) and *Megalichthys* appear to have been better adapted to marine environments, while some other fishes (*Rhizodus*, *Rhizodopsis*) appear to be better suited to life in brackish tidal estuaries based on facies distribution data (Table 2). This heterogeneity is reflected by the Simpson Index, which shows that fish diversity declines from open marine environments towards more variably saline estuaries, suggesting that not all taxa were equally successful at infiltrating brackish water coastal tracts.

Aquatic tetrapod remains (embolomeres, colosteids), by contrast, are found only in brackish water facies and were probably euryhaline, hunting with in coastal brackish bays. This hypothesis has been raised, periodically, based on anecdotal facies associations across Euramerica (Milner 1987; Laurin and Soler-Gijon 2001; Schultze 2009), and is here supported, based on analysis of parautochthonous assemblages associated with a brackish water fauna. Embolomeres and colosteids have always been identified as primarily aquatic forms. The embolomeres, typically 1–4 m long, with their short limbs, elongate, laterally flexible trunks, and long flat-sided tails, have always been interpreted as largely aquatic predators on fishes of all sizes (Milner 1987). Likewise, colosteids were long-bodied, flat-headed predators up to 1 m in length, with reduced limbs and prominent lateral line systems,

both indicators of a primarily aquatic lifestyle (Milner 1987). Further, Milner (1987) notes the prevalence of a tetrapod association comprising embolomeres, keraterpetontid nectrideans, lysorophians, and trimerorachoid temnospondyls in Pennsylvanian assemblages throughout Europe and North America; these have been interpreted as salinity-tolerant organisms, indicating brackish conditions (Schultze, 2009, 2013). Our findings suggest that early tetrapods, either retained the osmoregulatory systems of their sarcopterygian ancestors, or independently diversified back into brackish settings.

The inferred widespread euryhalinity of Carboniferous fish and tetrapods in the Minto Formation contributes to the long-running debate regarding ecology. If taxa were freely migrating beneath marine and freshwater settings, or even occupying brackish coastal settings, it is possible for them to both have a marine-based dispersal pattern, explaining the cosmopolitan nature of assemblages (Sahney *et al*. 2010; Carpenter *et al*. 2015). However, a euryhaline habit, also, explain how such fishes and tetrapods could show enriched strontium isotope values indicative of continental/freshwater influences (Fischer *et al.* 2011, 2013; Montañez and Cecil 2013).

Evolutionary implications

The Maritimes Basin of Canada is a particularly informative area for studying the evolution of fish populations within brackish coastal waters. This depocentre is positioned near the continental interior of Pangaea (Falcon-Lang *et al.* 2006) but was intermittently connected to marine water bodies in the course of glacio-eustatic and tectonic fluctuations (Gibing *et al.* 2008). Fully marine incursions occurred only during three brief intervals, during part of the Visean (Windsor Group), the Bashkirian (Joggins and Tynemouth Creek formations; Grey *et al.* 2011; Falcon-Lang *et al*. 2015*b*) and early Moscovian stages (Minto Formation; this paper). However, brackish incursions were far more common, spanning the entire

Carboniferous interval (Archer *et al.* 1995; Tibert and Scott 1999; Falcon-Lang *et al.* 2006; McIlroy and Falcon-Lang 2006; Gibling *et al.* 2008), and reflecting the periodic development of a brackish epicontinental sea, in some ways, analogous to the present-day Baltic Sea (Calder 1998; Falcon-Lang 2005). These brackish-marine incursions contain rich but fragmentary fish faunas (summarised in Fig. 17; see references in figure caption). A remarkable feature of these faunas in their conservative composition, with a consistent collection of taxa assembled by Serpukhovian times (Pomquet Formation) and persisting for 20 millon years, with minimal variation, until late Moscovian times (Sydney Mines Formation). Conservative composition was probably maintained by euryhalinity, which kept populations well mixed, and suppressed allopatric speciation.

CONCLUSIONS

1. We describe a new fish and tetrapod assemblage from the Carboniferous (Pennsylvanian; early Moscovian) Minto Formation of New Brunswick, Canada.
2. The fish fauna includes chondrichthyans (xenacanthids, and the enigmatic *Ageleodus*), acanthodians (gyracanthids and acanthodiforms), sarcopterygians (rhizodontids, megalichthyids, rhizodopsids, dipnoans), and actinopterygians (eurynotiforms).
3. The tetrapod fauna includes small to medium-sized, and largely aquatic, forms of stem tetrapods (colosteids) and anthracosaurs (embolomeres).
4. Facies analysis of taxa across a brackish-marine palaeosalinity gradient demonstrate that almost all fish and tetrapod taxa were euryhaline, with chondrichthyans especially well equipped to traverse into non-marine environments.
5. Documentation of widespread euryhalinity in fish may explain how strontium isotope analyses of tooth enamel indicate continental influence when other data point to marine dispersal.

6. In the context of other rich Carboniferous fish faunas of the Maritimes Basin of Atlantic Canada, fossils show the assembly of a conservative range of euryhaline taxa over the 20 million year period coinciding with the mid-Carboniferous diversification.

Acknowledgements. AÓG gratefully acknowledges receipt of the Bob Savage Memorial Fund (University of Bristol) and funding from the New Brunswick Museum Creative Futures Fund and the Geological Surveys Branch of the New Brunswick Department of Energy and Mines to cover his fieldwork costs in 2015. HFL gratefully acknowledges a NERC Advanced Fellowship (NE/F014120/2) at Royal Holloway to conduct field research in Atlantic Canada. PKP gratefully acknowledges a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada. Michele Coleman (New Brunswick Coal) kindly facilitated access to geological datasets. Michelle Hébert (New Brunswick Museum) assisted with specimens. Discussion with Martin Gibling (Dalhousie University), together with the comments of two reviewers, greatly improved this paper. Lastly, we especially thank Michael Lee for donation of the fossil collections, which form the focus of this paper, to the New Brunswick Museum. We also thank Tim Smithson and an anonymous referee for their very helpful advice on the MS.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:

http://dx.doi.org/10.5061/dryad.xxxx

REFERENCES

AGASSIZ, L. J. R. 1843*a* (1837–1843). *Recherches sur les poissons fossiles*, **3**. Petitpierre, Neuchâtel et Soleure, viii + 390 + 32 pp.

— 1843*b* (1837–1843). *Recherches sur les poissons fossiles*, **2**. Petitpierre, Neuchâtel et Soleure, xii + 310 + 336 pp.

AHLBERG, P. E. 1991. A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society*, **103**, 241–287.

ALGEO, T. J. and SCHECKLER, S. E. 1998. Terrestrial-marine telecommunications in the Devonian: Links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society, London, Series B*, **353**, 113–130.

ANDERSON, L. I. and SHUSTER, C. N. 2003. Throughout geological time: where have they lived. *In* SHUSTER, C. N., BARLOW, R. B., and BROCKMANN, H. J. (eds.), *The American Horseshoe Crab.* Harvard University Press, Cambridge, Massachusetts, 189–223.

ANDERSSON, P. S., WASSERBURG, G. J. and INGRI, J. 1992. The sources and transport of Sr and Nd isotopes in the Baltic Sea. *Earth and Planetary Science Letters*, **113**, 459–472.

— , — and STORDAL, M. C. 1994. Strontium, dissolved and particulate loads in fresh and brackish waters: the Baltic Sea and Mississippi Delta. *Earth and Planetary Science Letters*, **124**, 195–210.

ANDREWS, S. M. 1985. Rhizodont crossopterygian fish from the Dinantian of Foulden, Berwickshire, Scotland, with a re-evaluation of this group. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 67–95.

— and WESTOLL, T. S. 1970. The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Transactions of the Royal Society of Edinburgh*, **68**, 391–489.

1137 ARCHER, A. W., CALDER, J. H., GIBLING, M. R., NAYLOR, R. D., REID, D. R. and
1138 WIGHTMAN, W. G. 1995. Invertebrate trace fossils and agglutinated foraminifera as
1139 indicators of marine influences within the classic Carboniferous section at Joggins, Nova
1140 Scotia, Canada. *Canadian Journal of Earth Sciences*, **32**, 2027–2039.
1141 BAILEY, L.W. and MATTHEW, G. F. 1873. Report of observations on the Carboniferous
1142 system of New Brunswick in the counties of Queens, Sunbury and a portion of York.
1143 *Geological Survey of Canada, Report of Progress for 1872–1873*, Part 8, 180–230.
1144 BAIRD, D. 1962. A haplolepid fish fauna in the Early Pennsylvanian of Nova Scotia.
1145 *Palaeontology*, **5**, 22–29.
1146 — 1978. Studies on Carboniferous freshwater fishes. *American Museum Novitates*, **1641**, 1–
1147 22.
1148 BALL, F. D., SULLIVAN, R. M. and PEACH, A. R. 1981. Carboniferous Drilling Project.
1149 Report Investigation 18. New Brunswick Department of Natural Resources, 109 pp.
1150 BARKAS, T. P. 1869. *Ctenodus interruptus*. *Scientific Opinion*, **2**, 113–114.
1151 BASHFORTH, A. R., CLEAL, C. J., GIBLING, M. R., FALCON-LANG, H. J., MILLER, R.
1152 F., 2014. Early Pennsylvanian plant communities on a seasonal tropical fluvial landscape
1153 (Tynemouth Creek Formation, New Brunswick, Canada). *Review of Palaeobotany and*
1154 *Palynology,* **200**, 229–263.
1155 BECK, K. G., SOLER-GIJÓN, R., CARLUCCI, J. R. and WILLIS, R. E. 2014. Morphology
1156 and histology of dorsal spines of the xenacanthid shark *Orthacanthus platypternus* from
1157 the Lower Permian of Texas, USA: palaeobiological and palaeoenvironmental
1158 implications. *Acta Palaeontologica Polonica*, **61**, 97–117.
1159 BENNETT, C. E., SIVETER, D.J., DAVIES, S. J., WILLIAMS, M., WILKINSON, I. P.,
1160 BROWNE, M. and MILLER, C. G. 2012. Ostracods from freshwater and brackish
1161 environments of the Carboniferous of the Midland Valley of Scotland: the early

1162 colonization of terrestrial water bodies. *Geological Magazine*, **149**, 366–396.
1163 BERG, L. S. 1937. A classification of fish-like vertebrates. *Bulletin de l'Académie des*
1164 *Sciences de l'URSS*, **20**, 1277–1280.
1165 — 1940. Classification of fishes, both living and fossil. *Trudy Zoologicheskovo Instituta*, **5**,
1166 85–517.
1167 BEZNOSOV, P. 2009. A redescription of the Early Carboniferous acanthodian *Acanthodes*
1168 *lopatini* Rohon, 1889. *Acta Zoologica*, **90**, 183–193.
1169 BINNEY, E. W. 1841. On the fossil fishes of the Pendleton coal field. *Transactions of the*
1170 *Manchester Geological Society*, **1**, 153–178.
1171 BOLT, J. R. and LOMBARD, R. E. 2010. *Deltaherpeton hiemstrae*, a new colosteid tetrapod
1172 from the Mississippian of Iowa. Journal of Paleontology, **84**, 1135–1151.
1173 BONAPARTE, C. L. 1838. *Iconografia della fauna Italiana per le quattro classi degli*
1174 *Animali Vertebrati, 3*. Salviucci, Rome, 266 pp.
1175 BRAZEAU, M. D. 2005. A new genus of rhizodontid (Sarcopterygii, Tetrapodomorpha) from
1176 the Lower Carboniferous Horton Bluff Formation of Nova Scotia, and the evolution of
1177 the lower jaws in this group. *Canadian Journal of Earth Sciences*, **42**, 1481–1499.
1178 — and WINTER, V. DE. 2015. The hyoid arch and braincase anatomy of *Acanthodes* support
1179 chondrichthyan affinity of "acanthodians". *Proceedings of the Royal Society B*, **282**,
1180 2015–2210.
1181 BUATOIS, L. A., MÁNGANO, M. G., GENISE, J. F. and TAYLOR, T. N. 1998. The
1182 ichnological record of the continental invertebrate invasion: evolutionary trends,
1183 environmental expansion, ecospace utilization, and behavioral complexity. *Palaios*, **13**,
1184 217–240.

—, GINGRAS, M. K., MACEACHERN, J., MÁNGANO, M. G., ZOONEVELD, J. P., PEMBERTON, S. G., NETTO, R. G., MARTIN, A., 2005. Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios*, **20**, 321–347.

BURROW, C. J., LONG, J. L. AND TRINAJSTIC, K. 2008. Disarticulated acanthodian and chondrichthyan remains from the upper Middle Devonian Aztec Siltstone, Southern Victoria Land, Antarctica. *Antarctic Science*, **21**, 71–88.

—, TURNER, S. and YOUNG, G. C. 2010. Middle Palaeozoic microvertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld*, **19**, 37–54.

CALDER, J. H. 1998. The Carboniferous evolution of Nova Scotia. 261–302. *In* BLUNDELL, D. J. and SCOTT, A. C. (eds.). *Lyell: the past is the key to the present.* Geological Society of London, Special Publication, **143**, 376 pp.

CALVER, M. A. 1968. Invertebrate faunas. 147–177. *In* MURCHISON, D. and WESTOLL, T. S. (eds.) *Coal and coal-bearing strata*. Oliver and Boyd, Edinburgh, 418 pp.

CAMPBELL, K. S. W. and DUY PHUOC, L. 1983. A late Permian actinopterygian fish from Australia. *Palaeontology*, **26**, 33–70.

—, and BARWICK, R. E. 2002. The axial postcranial structure of *Griphognathus whitei* from Gogo. Records of the Western Australian Museum, 21, 167–201.

CARPENTER, D. K., FALCON-LANG, H. J., BENTON, M. J. and NELSON, W. J. 2011. Fishes and tetrapods from the Pennsylvanian (Kasimovian) Cohn Coal Member of the Mattoon Formation, Illinois, USA: systematics, palaeoecology and palaeoenvironments. *Palaios*, **26**, 639–658.

—, —, —, and HENDERSON, E. 2014. Carboniferous (late Tournaisian) fish assemblages from the Isle of Bute, Scotland: systematics and palaeoecology. *Palaeontology*, **57**, 1215–1240.

—, —, —, and GREY, M. 2015. Early Pennsylvanian (Langsettian) fish assemblages from the Joggins Formation, Canada, and their implications for palaeoecology and palaeogeography. *Palaeontology*, **58**, 661–690.

CARROLL, R. L., 2009. The Rise of Amphibians: 365 Million Years of Evolution. The Johns Hopkins University Press, 544 pp.

—, BELT, E. S., DINELEY, D. L., BAIRD, D. and MCGREGOR, D. C. 1972. *Field excursion A59, vertebrate paleontology of Eastern Canada*, *guidebook*. 24th International Geological Congress, Montreal, 113 pp.

CHOO. B. 2011. Revision of the actinopterygian genus *Mimipiscis* (=*Mimia*) from the Upper Devonian Gog formation of Western Australia and the interrelationships of the early Actinopterygii. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **102**, 77–104.

— 2015. A new species of the Devonian actinopterygian *Moythomasia* from Bergisch Gladbach, Germany, and fresh observations on *M. durgaringa* from the Gogo Formation of Western Australia. *Journal of Vertebrate Paleontology*, **35**, e952817 (doi: 10. 1080/02724634.2015.952817).

—, LONG, J.A. and TRINAJSTIC, K. 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. *Acta Zoologica*, **90** (Suppl 1), 194–210.

CLARK, P. 2004. *The Sedimentology of Minto Salmon Harbour Mine site and its high sulfur coals*. Unpublished Honours thesis, University of New Brunswick, Fredericton, New Brunswick, 74 pp.

1231 COATES, M. I., RUTA, R. and FRIEDMAN, M. 2008. Ever since Owen: changing
1232 perspectives on the early evolution of tetrapods. *Annual Review of Ecology, Evolution*
1233 *and Systematics*, **39**, 571–592.
1234 COPE, E. D. 1887. Geology and palaeontology. *American Naturalist*, **1887**, 1014–1019.
1235 COSTAIN, T. 2000. *Stratigraphic analysis and possible tidal influences in the Thorburn*
1236 *Member and Coal Brook Member, Stellarton Formation, Nova Scotia.* Unpublished BSc
1237 thesis, Dalhousie University, 77 pp.
1238 DAVIES, N. S. and SANSOM, I. J. 2009. Ordovician Vertebrate Habitats: A Gondwanan
1239 Perspective. *Palaios*, **24**, 717–722.
1240 — and GIBLING, M. R. 2013. The sedimentary record of Carboniferous rivers: continuing
1241 influence of land plant evolution on alluvial processes and Palaeozoic ecosystems. *Earth*
1242 *Science Reviews*, **120**, 40–79
1243 DAVIES, S. J. and GIBLING, M. R. 2003. Architecture of coastal and alluvial deposits in an
1244 extensional basin: the Carboniferous Joggins Formation of eastern Canada.
1245 *Sedimentology*, 50, 415–439.
1246 DAWSON, J. W. 1868. *Acadian Geology* or *The Geology of Nova Scotia, New Brunswick and*
1247 *Prince Edward Island*, 2nd Edition. Oliver and Boyd, Edinburgh, 694 p.
1248 DENISON, R. 1979. Acanthodii. 1–62. *In* SCHULTZE, H-P. (ed.). *Handbook of*
1249 *Paleoichthyology Volume 5*. Gustav Fischer Verlag, Stuttgart and New York, 62 pp.
1250 DICK, J. R. F. 1981. *Diplodoselache woodi* gen. et sp. nov., an early Carboniferous shark
1251 from the Midland Valley of Scotland. *Transactions of the Royal Society of Edinburgh,*
1252 *Earth Sciences*, **72**, 99–113.
1253 DOWNS, J. P. and DAESCHLER, E. B. 2001. Variation within a large sample of *Ageleodus*
1254 *pectinatus* teeth (Chondrichthyes) from the late Devonian of Pennsylvania, USA. *Journal*
1255 *of Vertebrate Paleontology*, **21**, 811–814.

1256 EDWARDS, S. L. and MARSHALL, W. S. 2013. Principles and patterns of osmoregulation
1257 and euryhalinity in fishes. 1–44. *In* McCORMICK, S. D., FARRELL, A.P., and
1258 BRAUNER, C.J. (eds.), *Fish Physiology, Vol. 32, Euryhaline Fishes*, Elsevier, New
1259 York.
1260 FALCON-LANG, H. J. 2005. Small cordaitalean trees in a marine-influenced coastal habitat
1261 in the Pennsylvanian Joggins Formation, Nova Scotia, Canada. *Journal of the Geological*
1262 *Society, London*, **162**, 485–500.
1263 — 2009. The earliest history of coal mining and grindstone quarrying at Joggins, Nova Scotia
1264 and its implications for the meaning of the place-name "Joggins". *Atlantic Geology*, **45**,
1265 1–21.
1266 — , BENTON, M. J., BRADDY, S. J. and DAVIES, S. J. 2006. The Pennsylvanian tropical
1267 biome reconstructed from the Joggins Formation of Canada. *Journal of the Geological*
1268 *Society, London*, **163**, 561–576.
1269 — , MINTER, N. J., BASHFORTH, A. R., GIBLING, M. R., MILLER, R. F. 2015*a*. Mid-
1270 Carboniferous diversification of continental ecosystems inferred from trace fossil suites in
1271 the Tynemouth Creek Formation of New Brunswick, Canada. *Palaeogeography,*
1272 *Palaeoclimatology, Palaeoecology*, **440**, 142–160.
1273 — , PUFAHL, P. K., BASHFORTH, A. R., GIBLING, M. R., MILLER, R. F. and MINTER,
1274 N.J. 2015*b*. A marine incursion in the Lower Pennsylvanian Tynemouth Creek
1275 Formation, Canada: implications for paleogeography, stratigraphy and paleoecology.
1276 *Palaios*, **30**, 779–791.
1277 FIELDING, C.R., FRANK, T.D., BIRGENHEIER, L.P., RYGEL, M.C., JONES, A.T. and
1278 ROBERTS, J. 2008. Stratigraphic imprint of the Late Palaeozoic Ice Age in eastern
1279 Australia: a record of alternating glacial and nonglacial climate regime. *Journal of the*
1280 *Geological Society*, **165**, 129–140.

1281 FISCHER, J., VOIGT, S., SCHNEIDER, J.W., BUCHWITZ, M. and VOIGT, S. 2011. A
1282 selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for
1283 Mesozoic shark nurseries. *Journal of Vertebrate Paleontology*, **31**, 937-953.
1284 —, SCHNEIDER, J. W., VOIGT. S., JOACHIMSKI, M. M., TICHOMIROWA, M.,
1285 TUTKEN, T., GOTZE, J. and BERNER, U. 2013. Oxygen and strontium isotopes from
1286 fossil shark teeth: Environmental and ecological implications for Late Palaeozoic
1287 European basins. *Chemical Geology*, **342**, 44–62.
1288 FOX, R. C., CAMPBELL, K. S. W., BARWICK, R. E. and LONG, J. A. 1995. A new
1289 osteolepiform fish from the Lower Carboniferous Raymond Formation, Drummond
1290 Basin, Queensland. *Memoirs of the Queensland Museum*, **38**, 99–221.
1291 FRIEDMAN, M., COATES, M. I. and ANDERSON, P. 2007. First discovery of a primitive
1292 coelacanth fin fills a major gap in the evolution of lobed fins and limbs. *Evolution and*
1293 *Development*, **9**, 328–336.
1294 — and SALLAN, L. C. 2012. Five hundred million years of extinction and recovery: a
1295 Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology*, **55**, 707–
1296 742.
1297 GAGNIER, P-Y. and WILSON, M. V. H. 1996. Early Devonian acanthodians from northern
1298 Canada. *Palaeontology*, **39**, 241–258.
1299 GARDINER, B. G. 1966. *Catalogue of Canadian fossil fishes.* Contribution No. 68, Life
1300 Sciences. Royal Ontario Museum, University of Toronto, 154 pp.
1301 — 1984. The relationship of the palaeoniscid fishes, a review based on new specimens of
1302 *Mimia* and *Moythomasia* from the Upper Devonian of western Australia. *Bulletin of the*
1303 *British Museum, Natural History (Geology)*, **37**, 173–428
1304 — and SCHAEFFER, B. 1989. Interrelationships of lower actinopterygian fishes. *Zoological*
1305 *Journal of the Linnean Society*, **97**, 135–187.

1306 GENSEL, P. G. and EDWARDS, D. 2001. *Plants invade the land*. Columbia University
1307 Press, New York, 304 pp.
1308 GESNER, A. 1841. *Third report on the Geological Survey of the Province of New Brunswick*.
1309 Henry Chubb, Saint John, New Brunswick, 88 pp.
1310 GIBLING, M. R. and KALKREUTH, W .D. 1991. Petrology of selected carbonaceous
1311 limestones and shales in Late Carboniferous coal basins of Atlantic Canada. *International*
1312 *Journal of Coal Geology*, **17**, 239–271.
1313 — and RUST, B. R. 1992. Silica-cemented palaeosols (ganisters) in the Pennsylvanian
1314 Waddens Cove Formation, Nova Scotia, Canada. *In* WOLF, K. H. and CHILINGARIAN,
1315 G. V. (eds), *Diagenesis III: Developments in Sedimentology 47*, Amsterdam, Elsevier, p.
1316 621–655.
1317 — CALDER, J. H., RYAN, R., VAN DER POLL, H. W. and YEO, G. M. 1992. Late
1318 Carboniferous and Early Permian drainage patterns in Atlantic Canada. *Canadian Journal*
1319 *of Earth Sciences*, **29**, 338–352.
1320 — CULSHAW, N., RYGEL, M. C. and PASCUCCI, V. 2008. The Maritimes Basin of
1321 Atlantic Canada: basin creation and destruction in the collisional zone of Pangea. 211–
1322 244. *In* MIALL, A. D. (ed.). *The sedimentary basins of the United States and Canada*.
1323 Elsevier, Oxford, 624 pp.
1324 GIERLOWSKI-KORDESCH, E. H. and CASSLE, C. F. 2015. The "*Spirorbis"* problem
1325 revisited: sedimentology and biology of microconchids in marine-nonmarine transitions.
1326 *Earth-Science Reviews*, **148**, 209–227.
1327 — FALCON-LANG, H. J. and CASSLE, C. F. 2016. Reply to comment on the paper of
1328 Gierlowski and Cassle, The "*Spirorbis"* problem revisited [Earth-Science Reviews, 148,
1329 209–227]. *Earth-Science Reviews*, **152**, 201–204.

1330 GOODRICH, E. S. 1930. Studies on the Structure and Development of Vertebrates.
1331 Macmillian and Co, London.
1332 GRAY, T. R., DOSTAL, J., McLEOD, M., KEPPIE, D. and ZHANG, Y. 2012. Geochemistry
1333 of Carboniferous peralkaline felsic volcanic rocks, central New Brunswick, Canada:
1334 examination of uranium potential. *Atlantic Geology*, **46**, 173–184.
1335 GREINER, H. 1977. Crossopterygian fauna from the Albert Formation, New Brunswick,
1336 Canada, and its stratigraphic-paleoecologic significance. *Journal of Paleontology*, **51**, 44–
1337 56.
1338 GREY, M., PUFAHL, P. K. and AZIZ, A. A. 2011. Using multiple environmental proxies to
1339 determine degree of marine influence and paleogeographical position of the Joggins
1340 Fossil Cliffs UNESCO World Heritage Site. *Palaios*, **26**, 256–263.
1341 HACQUEBARD, P. A. and BARSS, M. S. 1970. Paleogeography and facies aspects of the
1342 Minto Coal seam, New Brunswick, Canada, C.R. *Sixth International Congress of*
1343 *Carboniferous Stratigraphy and Geology*, **3**, 861–872.
1344 HAMPE, O. 1988. Über die Bezahnung des *Orthacanthus* (Chondrichthyes: Xenacanthida;
1345 Oberkarbon-Unterperm). *Paläontologische Zeitschrift*, **62**, 285–296.
1346 — 2002. Revision of the Xenacanthida (Chondrichthyes: Elasmobranchii) from the
1347 Carboniferous of the British Isles. *Earth and Environmental Science Transactions of the*
1348 *Royal Society of Edinburgh*, **93**, 191-237.
1349 HANCOCK, A. and ATTHEY, T. 1870. Note on an undescribed fossil fish from the
1350 Newsham coal-shale near Newcastle-upon-Tyne. *Annals and Magazine of Natural*
1351 *History Series 4*, **5**, 266–268.
1352 HANKE, G. F. 2008. *Promesacanthus eppleri* n. gen., n. sp., a mesacanthid (Acanthodii,
1353 Acanthodiformes) from the Lower Devonian of northern Canada. *Geodiversitas*, **30**, 287–
1354 302.

1355 HAY, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America.
1356 *Bulletin of the United States Geological Survey*, **179**, 1–868.
1357 HEIDKE, U. H. J. 1998. Revision of the genus *Orthacanthus* Agassiz 1843 (Chondrichthyes:
1358 Xenacanthida). *Paläontologische Zeitschrift*, **72**, 135–147.
1359 HOLLAND, T., WARREN, A., JOHANSON, Z., LONG, J., PARKER, K. and GARVEY, J.
1360 2007. A new species of *Barameda* (Rhizodontida) and heterochrony in the rhizodontid
1361 pectoral fin. *Journal of Vertebrate Paleontology*, **27**, 295–315.
1362 — LONG, J. and SNITTING, D. 2010. New information on the enigmatic tetrapodomorph
1363 fish *Marsdenichthys longioccipitus* (Long 1985). *Journal of Vertebrate Paleontology*, **30**,
1364 68–77.
1365 HUNT, A. P. and LUCAS, S. G. 2012*a*. Descriptive terminology of coprolites and Recent
1366 feces. *New Mexico Museum of Natural History and Science, Bulletin*, **57**, 153–160.
1367 — and — 2012*b*. Classification of vertebrate coprolites and related trace fossils. *New Mexico*
1368 *Museum of Natural History and Science, Bulletin*, **57**, 137–146.
1369 —, —, SPIELMANN, J. A., CANTRELL, A., SUAZO, T. and LERNER, A. J. 2012.
1370 Bromalites from the Tinajas Lagerstätte (Late Pennsylvanian: Late Missourian), central
1371 New Mexico, USA. *New Mexico Museum of Natural History and Science, Bulletin*, **57**,
1372 175–183.
1373 HUXLEY, T. H. 1861. Preliminary essay on the systematic arrangement of the fishes of the
1374 Devonian epoch. Figures and descriptions illustrative of British organic remains. Decade
1375 10. *Memoirs of the Geological Survey of the United Kingdom*, London, 1-40.
1376 — 1880. On the application of the laws of evolution to the arrangement of the Vertebrata,
1377 and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*,
1378 **1880**, 649–662.

— and ETHERIDGE, R. 1865. *A catalogue of the collection of fossils in the Museum of Practical Geology, with an explanatory introduction*. G. E. Eyre and W. Spottiswoode, London, 381 pp.

JANVIER, P. 1996. *Early vertebrates*. Oxford Monographs on Geology and Geophysics, **33**, 393 pp.

JEFFERY, J. E. 2003. Mandibles of rhizodontids: anatomy, function, and evolution within the tetrapod stem-group. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **93**, 255–276.

— 2006. The Carboniferous fish genera *Strepsodus* and *Archichthys* (Sarcopterygii: Rhizodontida): clarifying 150 years of confusion. *Palaeontology*, **49**, 113–132.

JEPPSSON, L., FREDHOLM, D. and MATTIASSON, B. 1985. Acetic acid and phosphatic fossils – a warning. *Journal of Paleontology*, **59**, 952–956.

JOHANSON, Z. and AHLBERG, P. E. 2001. Devonian rhizodontids and tristichopterids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **92**, 43–74.

JOHNSON, G. D. 1979. *Early Permian vertebrates from Texas: Actinopterygii (Schaefferichthys), Chondrichthyes (including North American Pennsylvanian and Triassic Xenacanthodii, and Acanthodii)*. Unpublished Ph.D. thesis, Southern Methodist University, Dallas, Texas, 653 pp.

— 1999. Dentitions of Late Palaeozoic *Orthacanthus* species and new species of ?*Xenacanthus* (Chondrichthyes: Xenacanthiformes) from North America. *Acta Geologica Polonica*, **49**, 215–266

— and ZIDEK, J. 1981. Late Paleozoic phyllodont tooth plates. *Journal of Paleontology*, **1981**, 524–536.

1403 JONES, B. and DIXON, O. A. 1977. Stratigraphy and sedimentology of upper Silurian rocks,
1404 northern Somerset Island, Arctic Canada. *Canadian Journal of Earth Sciences*, **14**, 1427–
1405 1452.
1406 KALKREUTH, W. MARCHIONI, D. and UTTING, J. 2000. Petrology, palynology, coal
1407 facies, and depositional environments of an Upper Carboniferous coal seam, Minto
1408 Coalfield, New Brunswick, Canada. *Canadian Journal of Earth Sciences*, **37**, 1209–1228.
1409 KARATAJUTE-TALIMAA, V. N. 1992. The early stages of the dermal skeleton formation in
1410 chondrichthyans. *In* MARK-KURIK, E. (ed.) *Fossil Fishes as Living Animals.*
1411 Proceedings of the II International Colloquium on the study of Palaeozoic fishes, Tallinn,
1412 1898. *Academia*, **1**, 223–231.
1413 KEMP, A. 1996. *Sagenodus* (*Proceratodus*) *carlinvillensis* (Romer and Smith 1934),
1414 (Osteichthyes: Dipnoi), short ridge anomaly and classification of dipnoans. *Journal of*
1415 *Vertebrate Paleontology*, **16**, 16–19.
1416 — 2003. Development anomalies in the tooth plates and jaw bones of lungfish. *Journal of*
1417 *Vertebrate Paleontology*, **23**, 517–531.
1418 KENNEDY, K. L., MILLER, R. F. and GIBLING, M. R. 2012. Palaeoenvironments of Early
1419 Devonian fish and other aquatic fauna of the Campbellton Formation, New Brunswick,
1420 Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 361–362, 61–72.
1421 KRIWET, J., WITZMANN, F., KLUG, S. and HEIDTKE, U. H. J. 2008. First direct evidence
1422 of a vertebrate three-level trophic chain in the fossil record. *Proceedings of the Royal*
1423 *Society B*, **275**, 181–186.
1424 LAMBE, L. M. 1910. Palaeoniscid fishes from the Albert Shales of New Brunswick.
1425 *Geological Survery of Canada, Contributions to Canadian Paleontology, Memoir*, **3**, 1–
1426 69.

1427 LEBEDEV, O. A. 1996. Fish assemblages in the Tournaisian – Viséan environments of the
1428 East European Platform. 387–415. *In* STROGEN, P., SOMERVILLE, I. D. and JONES,
1429 G. Ll. (eds.). *Recent advances in Lower Carboniferous geology*. Geological Society
1430 Special Publication **107**, The Geological Society Publishing House, Bath, 464 pp.
1431 LEE, C. E. and BELL, M. A. 1999. Causes and consequences of recent freshwater invasions
1432 by saltwater animals. *Trends in Ecology and Evolution*, **14**, 284-288.
1433 LONG, J. A. 1986. A new Late Devonian acanthodian fish from Mt. Howitt, Victoria,
1434 Australia, with remarks on acanthodian biogeography. *Proceedings of the Royal Society*
1435 *of Victoria*, **98**, 1–17.
1436 MacNAUGHTON, R. B., COLE, J. M., DALRYMPLE, R. W., BRADDY, S. J., BRIGGS, D.
1437 E. G., and LUKIE, T. D. 2002. First steps on land: arthropod trackways in Cambrian-
1438 Ordovician eolian sandstone, southeastern Ontario, Canada. *Geology*, **30**, 391–394.
1439 MALIVA, R. G. 1989. Displacive calcite syntaxial overgrowths in open marine limestones.
1440 *Journal of Sedimentary Research*, **59**, 397–403.
1441 MANSKY, C. F. and LUCAS, S. G. 2013. Romer's Gap revisited: continental assemblages
1442 and ichno-assemblages from the basal Carboniferous of Blue Beach, Nova Scotia,
1443 Canada. *In* LUCAS, S. G., DiMICHELE, W. A., BARRICK, J. E., SCHNEIDER, J. W.
1444 and SPEILMAN, J. A. (eds.) *The Carboniferous–Permian Transition.* New Mexico
1445 Museum of Natural History and Science, **60**, 244–273.
1446 MASSON, A. G. and RUST, B. R. 1984. Freshwater shark teeth as environmental indicators
1447 in the Upper Pennsylvanian coal-bearing succession near Sydney, Nova Scotia. *Canadian*
1448 *Journal of Earth Sciences*, **21**, 1151–1155.
1449 McALLISTER, J. A. 1985. Reevaluation of the formation of spiral coprolites. *The University*
1450 *of Kansas Paleontological Contributions*, *Paper,* **114**, 1–12.

— 1987. Phylogenetic distribution and morphological reassessment (SIC) of the intestines of fossil and modern fishes. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **115**, 281–294.

McCORMICK, S. D., FARRELL, A. P. and BRAUNER, C. J. (eds) 2013. *Euryhaline fishes*. *Fish Physiology*, **32**, Elsevier, London, 594 pp.

McILROY, D. and FALCON-LANG, H. J. 2006. Discovery and paleoenvironmental implications of a *Zoophycos*-group trace fossil (? *Echinospira*) from the Middle Pennsylvanian Sydney Mines Formation of Nova Scotia. *Atlantic Canada*, **42**, 31–35.

MICKLE, K. E. and BADER, K. 2009. A new Platysomid from the Upper Carboniferous of Kansas (USA) and remarks on the systematics of deep-bodied lower actinopterygians. *Acta Zoologica*, **90**, 211–219.

MILLER, R. F. 1999. Report of *Gyracanthus* (Chordata: Acanthodii) and other Upper Carboniferous fish from the Minto Formation, New Brunswick (NTS 21 1/4). 37–43. *In* CARROLL, B. M. W. (ed.). *Current Research 1998*. New Brunswick Department of Natural Resources and Energy, Minerals and Energy Division, Mineral Resource Report **99-4**, New Brunswick Department of Natural Resources and Energy, Fredericton, 163 pp.

— and FORBES, W. H. 2001. An Upper Carboniferous trigonotarbid, *Aphantomartus pustulatus* (Scudder 1884) from the Maritimes Basin (Euramerican Coal Province), New Brunswick, Canada. *Atlantic Geology*, **37**, 191–196.

— and McGOVERN, J. H. 1997. Preliminary report of fossil fish (Actinopterygii: Palaeonisciformes) from the Lower Carboniferous Albert Formation at Norton, New Brunswick (NTS 21 H/12). *In* CARROLL. B. M. W. (ed.) *Current Research 1996*. New Brunswick Department of Natural Resources, Resource Report, **97**, 191–200.

MILLER, M. F. and LABANDEIRA, C. C. 2002. Slow crawl across the salinity divide: delayed colonization of freshwater ecosystems by invertebrates. *GSA Today*, **12**, 4–10.

1476 MILNER, A. R. 1987. The Westphalian tetrapod fauna; some aspects of its geography and
1477 ecology. *Journal of the Geological Society, London*, **144**, 495–506.
1478 MINTER, N. J., BUATOIS, L. A., MÁNGANO, M. G., DAVIES, N. S., GIBLING, M. R.
1479 and LABANDEIRA, C. C. 2016. The establishment of terrestrial ecosystems. In:
1480 MÁNGANO, M.G. and BUATOIS, L.A. (eds.), The trace-fossil record of major
1481 evolutionary events. Topics in Geobiology 39, xxx–xxx. Springer.
1482 MONTAÑEZ, I. P. and CECIL, C. B. 2013. Paleoenvironmental clues archived in non-marine
1483 Pennsylvanian-lower Permian limestones of the Central Appalachian Basin, USA.
1484 *International Journal of Coal Geology*, **119**, 41–55.
1485 — and POULSEN, C.J. 2013. The Late Paleozoic Ice Age: an evolving paradigm. *Annual*
1486 *Review of Earth and Planetary Sciences*, **41**, 629–656.
1487 MOY-THOMAS, J. A. 1937. The Palaeoniscids from the Cement Stones of Tarras Waterfoot,
1488 Eskdale, Dumfriesshire. *Journal of Natural History*, **20**, 345–356.
1489 MÜLLER, J. 1845. Über den Bau und die Grenzen der Ganoiden, und über das natürliche
1490 System der Fische. *Archiv für Naturgeschichte*, **1845**, 91–142.
1491 NAYLOR, R. D., ARCHER, A. W., CHANDLER, F. W. and FRALICK, P. W. 1998.
1492 Fluvioestuarine sedimentation in the Late Carboniferous Malagash Formation of Nova
1493 Scotia, Canada. *Nova Scotia Department of Natural Resources, Report of Activities 1998*,
1494 Report ME 1999-1, p. 71–89.
1495 NELSON, J. S. 1976. *Fishes of the world.* Wiley & Sons, New York, 416 pp.
1496 NEWBERRY, J. S. 1856. Description of several new genera and species of fossil fishes, from
1497 the Carboniferous strata of Ohio. *Proceedings of the Academy of Natural Sciences of*
1498 *Philadelphia*, **8**, 96–100.
1499 Ó GOGÁIN, A., FALCON-LANG, H. J., CARPENTER, D. K., MILLER, R. F., BENTON,
1500 M. J., PUFAHL, P. K., RUTA, M., DAVIES, T., HINDS, S. J. and STIMSON, M. R.

2016. Data from: Fish and tetrapod communities across a marine to brackish salinity gradient in the Pennsylvanian (early Moscovian) Minto Formation of New Brunswick, Canada, and their palaeoecological and palaeogeographic implications. *Dryad Digital Repository*. doi: 10.5061/dryad.xxxx

ØRVIG, T. 1978. Microstructure and growth of the dermal skeleton in fossil actinopterygian fishes: *Nephrotus* and *Colobodus*, with remarks on the dentition in other forms. *Zoologica Scripta*, **7**, 297–326.

OWEN, R. 1840. *Odontography; or, a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure in the vertebrate animals. Volume 1, text*. Hippolyte Baillière, London, 655 pp.

— 1846. *Lectures on the comparative anatomy and physiology of the vertebrate animals delivered at the Royal College of Surgeons, England in 1844 and 1846*. Part 1, fishes. Longman, Brown, Green and Longmans, London, 304 pp.

— 1867. On the dental characters of genera and species, chiefly of fishes, from the Low Main Seam and shales of coal, Northumberland. *Transactions of the Odontological Society of Great Britain*, **1**, 323–391.

PAGEAU, Y. 1969. Nouvelle faune ichthyologique du Dévonien moyen dans les Grès de Gaspé (Québec). II. Morphologie et systématique. Première section: A. Euryptérides, B. Ostracodermes, C. Acanthodiens et Sélaciens. *Naturaliste Canadien*, **96**, 399–478.

PARK, L. E. and GIERLOWSKI-KORDESCH, E. H. 2007. Paleozoic lake faunas: establishing aquatic life on land. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **249**, 160–179.

PATTERSON, C. 1982. Morphology and interrelationship of primitive actinopterygian fishes. *American Zoologist*, **22**, 241–259.

1525 PAWLEY, K. and WARREN, A. A. 2006. The appendicular skeleton of Eryops
1526 megacephalus Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of
1527 North America. *Journal of Paleontology*, **80**, 561–580.
1528 PETERSON, J. A. 2011. Better mathematical constraints on ages of Carboniferous stage
1529 boundaries using radiometric tuff dates and cyclostratigraphy. *Geochemistry, Geophysics,*
1530 *Geosystems*, **12**, Q0AA15, doi: 10.1029/2010GC003467.
1531 POINTON, M. A., CHEW, D. M., OVTCHAROVA, M., SEVASTOPULO, G. D. and
1532 CROWLEY, Q. G. 2012. New high-precision U-Pb dates from western European
1533 Carboniferous tuffs; implications for time scale calibration, the periodicity of late
1534 Carboniferous cycles and stratigraphical correlation. *Journal of the Geological Society*,
1535 **169**, 713–721.
1536 PORTLOCK, J. E. 1843. *Report on the geology of the County of Londonderry, and of parts of*
1537 *Tyrone and Fermanagh*. A. Milliken, Dublin, 784 pp.
1538 PRESCOTT, Z., STIMSON, M. R., DEFOE, L. T., GIBLING, M. R., MACRAE, R. A.,
1539 CALDER, J. H. and HEBERT, B. 2014. Microbial mats and ichnofauna of a fluvial-tidal
1540 channel in the Lower Pennsylvanian Joggins Formation, Canada. *Palaios*, **29**, 624–645.
1541 QUANN, S., YOUNG, A., LAROQUE, C., FALCON-LANG, H. J. and GIBLING, M. R.
1542 2010. Dendrochronologic dating of coal mine workings at the famous Joggins Fossil
1543 Cliffs of Nova Scotia, Canada. *Atlantic Geology*, **46**, 185–194.
1544 RICHARDS, B. C. 2013. Current status of the international Carboniferous time scale. *New*
1545 *Mexico Museum of Natural History and Science, Bulletin*, **60**, 348–353.
1546 ROBB, J. 1850. Report of coal in New Brunswick. 38–47. *In* JOHNSTON, J.F.W. (ed) *Report*
1547 *of the Agricultural Capabilities of the Province of New Brunswick.* Queen's Printer,
1548 Fredericton, New Brunswick.

1549 ROHON, J. V. 1889. Über fossile Fische vom oberen Jenissei. *Memoires de l'Académie*
1550 *Impériale des Sciences de St-Pétersbourg, VII Série*, **36**, 1–17.
1551 ROMER, R. S. 1955. *Herpetichthys*, Amphiboidei, Choanichthyes or Sarcopterygii? *Nature*,
1552 **176**, 126–127.
1553 RUST, B. R. and GIBLING, M. R. 1990. Braidplain evolution in the Pennsylvanian South Bar
1554 Formation, Sydney Basin, Nova Scotia, Canada. *Journal of Sedimentary Research*, **1**, 59–
1555 72.
1556 RYGEL, M. C., FIELDING, C. R., FRANK, T. D. and BIRGENHEIER, L. P. 2008. The
1557 magnitude of Late Paleozoic glacioeustatic fluctuations: a synthesis. *Journal of*
1558 *Sedimentary Research*, **78**, 500–511.
1559 SAHNEY, S., BENTON, M. J. and FALCON-LANG, H. J. 2010. Rainforest collapse
1560 triggered Carboniferous tetrapod diversification in Euramerica. *Geology*, **38**, 1079–1082.
1561 SALLAN, L. C. 2014. Major issues in the origin of ray-finned fish (Actinopterygii)
1562 biodiversity. *Biological Reviews*, **89**, 950–971.
1563 — and COATES, M. I. 2010. End-Devonian extinction and a bottleneck in the early evolution
1564 of modern jawed vertebrates. *Proceedings of the National Academy of Sciences, USA*,
1565 **107**, 10131–10135.
1566 — , — 2013. Styracopterid (Actinopterygii) ontogeny and the multiple origins of post-
1567 Hangenburg deep-bodied fishes. *Zoological Journal of the Linnean Society*, **169**, 156–199.
1568 — , — 2014. The long-rostrumed elasmobranch *Bandringa* Zangrel, 1969, and taphomomy
1569 within a Carboniferous shark nursery. *Journal of Vertebrate Paleontology*, **34**, 22–33.
1570 SANSOM, I. J., MILLER, C. G., HEWARD, A., DAVIES, N.S., BOOTH, G. A., FORTEY,
1571 R. A., and PARIS, F. 2009.Ordovician fish from the Arabian Peninsula. *Palaeontology*,
1572 **52**, 337–342.

SCHIEBER, J. 2002, Sedimentary pyrite: a window into the microbial past. *Geology*, **30**, 531–534.

SCHMITZ, B., ABERG, G., WERDLIN, L., FOREY, P. and BENDIX-ALMGREEN, S. E. 1991. $^{87}Sr/^{86}Sr$, Na, F, Sr, and La in skeletal fish debris as a measure of the paleosalinity of fossil–fish habitats. *Geological Society of America Bulletin*, **103,** 786–794.

SCHNEIDER, J. W., HAMPE, O. and SOLER-GIJÓN, R. 2000. The Late Carboniferous and Permian: Aquatic vertebrate zonation in southern Spain and German basins. *Courier Forschungsinstitut Senckenberg,* **223**, 543-61.

SCHULTZ, E.T. and McCORMICK, S.D. 2013. Euryhalinity in an evolutionary context. *EEB Articles*, Paper 29.

SCHULTZE, H.–P. 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Ubergang von Ganoid- zu Rund-Schuppen). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **126**, 232–314.

— 1970. Folded teeth and the monophyletic origin of tetrapods. *American Museum Novitates*, **2408**, 1–10

— 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläontologische Zeitschrift*, **51**, 152–168.

— 2009. Interpretation of marine and freshwater paleoenvironments in Permo-Carboniferous deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **281**, 126–136.

— and CHORN, J. 1986. Palaeoniscoid (Actinopterygii, Pisces) vertebrae from the Late Paleozoic of central North America. *Journal of Paleontology*, **60**, 744–757.

— and — 1997. The Permo-Carboniferous genus *Sagenodus* and the beginning of modern lungfish. *Contributions to Zoology*, **67**, 9–70.

SHARP, E. L. and CLACK, J. A. 2013. A review of the Carboniferous lungfish *Ctenodus* Agassiz, 1838 from the United Kingdom, with new data from an articulated specimen of

Ctenodus interruptus Barkas, 1869. *Transactions of the Royal Society of Edinburgh: Earth and Environmental Sciences*, **104**, 169–204.

SMITH, G. 1989. Coal in Canada. *Geological Survey of Canada, Paper* 89-4.

SNYDER, D. 2011. Gyracanthid gnathostome remains from the Carboniferous of Illinois. *Journal of Vertebrate Paleontology*, **31**, 902–906.

SOLER-GIJÓN, R. 1995. Evidence of predator–prey relationship in xenacanth sharks of the Upper Carboniferous (Stephanian C) from Puertollano, Spain. *Geobios*, **19**, 151–156.

ST. PETER, C. 1997. Bedrock geology of the Chipman/Canaan River map area (NTS 21 I/04 and part of 21 H/13), Sunbury, Queens and Kings counties, New Brunswick. *New Brunswick Department of Natural Resources and Energy, Minerals and Energy Division*, Plate 97-34.

— 2000. Carboniferous geology of the southwestern New Brunswick platform (Maugerville Subbasin). *New Brunswick Department of Natural Resources and Energy, Mineral Resources*, Plate 2000-16.

—, and JOHNSON, S.C. 2009. Stratigraphy and structural history of the late Paleozoic Maritimes Basin in southeastern New Brunswick, Canada. New Brunswick. *Department of Natural Resources; Minerals, Policy and Planning Division, Memoir*, **3**, 348 p.

ŚTAMBERG, S. and ZAJÍC, J. 2008. *Carboniferous and Permian faunas and their occurrence in the limnic basins of the Czech Republic*. Museum of Eastern Bohemia. 224 pp.

STERNBERG, R. M. 1941. Carboniferous dipnoans from Nova Scotia. *American Journal of Science*, **239**, 836–838.

SUES, H.-D., HOOK, R. W. and OLSEN, P. E. 2013. Donald Baird and his discoveries of Carboniferous and early Mesozoic vertebrates in Nova Scotia. *Atlantic Geology*, **49**, 90–103.

SULLIVAN, R.M. 1981. *A brief petrographic study of the rock stratigraphic unit Mississippian-Pennsylvanian felsic volcanics (MPfv) near Stanley, New Brunswick.* Supplementary Report No. 4 of the Carboniferous Drilling Project, New Brunswick Department of Natural Resources, Mineral Development Branch, Open File Report 81 3, 20 pp.

THOMPSON, K. S. 1964. Revised generic diagnoses of the fossil fishes *Megalichthys* and *Ectosteorhachis* (family Osteolepidae). *Bulletin of the Museum of Comparative Zoology*, **131**, 283–311.

TIBERT, N. E. and SCOTT, D. B. 1999. Ostracodes and agglutinated foraminifera as indicators of paleoenvironmental change in an Early Carboniferous brackish bay, Atlantic Canada. *Palaios*, **14**, 246–260.

TRAQUAIR, R. H. 1881*a*. Report on the fossil fishes collected by the Geological Survey of Scotland in Eskdale and Liddlesdale, part 1, Ganoidei. *Edinburgh Philosophical Transactions*, **30**, 15–71.

— 1881*b*. On the cranial osteology of *Rhizodopsis*. *Transactions of the Royal Society of Edinburgh*, **30**, 167–179.

— 1890. Observations on some fossil fishes from the Lower Carboniferous rocks of Eskdale, Dumfriesshire. *Annals and Magazine of Natural History (6th series)*, 6, 491–494.

TUCKER, M.E. and WRIGHT, V.P. 1990. *Carbonate Sedimentology*. Blackwell Scientific Publications, London, 482 pp.

TURNER, S. 2013. *Ageleodus*: widespread mid-Palaeozoic sharks known only from teeth. 61st Symposium on Vertebrate Palaeontology and Comparative Anatomy, Abstracts with Programme, Edinburgh, p. 43.

— , BURROW, C. and WARREN, A. 2005. *Gyracanthides hawkinsi* sp. nov. (Acanthodii, Gyracanthidae) from the Lower Carboniferous of Queensland, Australia, with a review of gyracanthid taxa. *Palaeontology*, **48**, 963–1006.

VAN DE POLL, H. W. 1973. Stratigraphy, sediment dispersal and facies analysis of the Pennsylvanian Pictou Group in New Brunswick. *Maritime Sediments*, **9**, 72–77.

VOROBYEVA, E. I. 1977. Evolutionary modifications of the teeth structure in the Palaeozoic Crossopterygii. *Journal of the Palaeontological Society of India*, **20**, 16-20

WARREN, A., CURRIE, B. P., BURROW, C. and TURNER, S. 2000. A redescription and reinterpretation of *Gyracanthides murrayi* Woodward 1906 (Acanthodii, Gyracanthidae) from the Lower Carboniferous of the Mansfield Basin, Victoria, Australia. *Journal of Vertebrate Paleontology*, **20**, 225–242.

WATERS, C. N. and CONDON, D. J. 2012. Nature and timing of Late Mississippian to Mid-Pennsylvanian glacio-eustatic sea-level changes of the Pennine Basin, UK. *Journal of the Geological Society of London*, **169**, 37–51.

WELLS, M. R., ALLISON, P. A., PIGGOTT, M. D., PAIN, C. C., HAMPSON, G. J. and DE OLIVIERA, C. R. E. 2005. Large sea, small tides: the Late Carboniferous seaway of NW Europe. *Journal of the Geological Society of London*, **162**, 417–420.

WILLIAMS, M., LENG, M. J., STEPHENSON, M. H., ANDREWS, J. E., WILKINSON, I. P., SIVETER, D. J., HORNE, D. J. and VANNIER, J. M. C. 2006. Evidence that Early Carboniferous ostracods colonised coastal flood plain brackish water environments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **230**, 299–318.

WILLIAMS, M. E. 1972. The origin of “spiral coprolites.” *The University of Kansas Paleontological Contributions*, **59**, 1–19.

WILLIAMS, S. C. and LUCAS, S. L. 2013. Taphonomy and paleoecology of Pennsylvanian fishes from Kinney Brick Quarry, New Mexico, USA. *In* LUCAS, S. G., NELSON, W. J.

, DiMICHELE, W. A., SPEILMAN, J. A., KRAINER, K., BARRICK, J. E., ELRICK, S., VOIGT, S. (eds.) *The Carboniferous–Permian Transition in Central New Mexico.* New Mexico Museum of Natural History and Science, **59**, 371–398.

WILLIAMSON, W. C. 1837. On the affinity of some fossil scales of fish from the Lancashire Coal Measures with those of the recent Salmonidæ. *Philosophical Magazine Series 3*, **11**, 300–301.

— 1849. On the microscopic structure of the scales and dermal teeth of some ganoid and placoid Fish. *Philosophical Transactions of the Royal Society of London*, **139**, 435–475.

WOODWARD, A. S. 1891. *Catalogue of the fossil fishes in the British Museum (Natural History). Part II. Containing the Elasmobranchii (Acanthodii), Holocephali, Ichthodorulites, Ostracodermi, Dipnoi and Teleostomi*. British Museum of Natural History, London, 553 pp.

— 1906. On a Carboniferous fish fauna from the Mansfield District, Victoria. *Memoirs of the National Museum of Victoria*, **1**, 1–32.

YOUNG, J. 1866. On the affinities of *Chondrosteus*, Ag. *Quarterly Journal of the Geological Society*, **22**, 569.

ZIDEK, J. 1976. Kansas Hamilton Quarry (Upper Pennsylvanian) *Acanthodes*, with remarks on the previously reported occurrences of the genus. *University of Kansas Paleontological Contributions*, **83**, 1–41.

— 1977. An acanthodid shoulder girdle from Lower Mississippian of Nova Scotia. *Journal of Paleontology*, **51**, 199–200.

— 1992. Late Pennsylvanian Chondrichthyes, Acanthodii, and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines and Mineral Resources Bulletin*, **138**, 145–182.

FIGURE CAPTIONS

FIG. 1. Location and geological context of the fossil sites. A, The Late Paleozoic Maritimes Basin of Atlantic Canada, developed in the oblique convergence zone of Laurasia and Gondwana (modified from Gibling *et al.* 2008). Inset map gives location within Canada. B, Geology of southern New Brunswick and northwest Nova Scotia showing the fossil sites near Grand Lake, positioned on the stable craton, adjacent to the active Moncton and Cumberland basins (modified from Falcon-Lang *et al.* 2015*a*). Other Pennsylvanian sites with marine beds (Joggins, Emerson Creek) are also shown. C, Geology of the Pennsylvanian (early Moscovian) Minto Coalfield of New Brunswick (after Hacquebard and Barss 1970; Ball *et al.* 1981; St Peter 2000) showing the location of the two fossil sites, borehole DH62-1 illustrated in Fig. 4, and other boreholes (closed circles). Abbreviations: NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island. Fig. 1 set for double column (166 mm).

FIG. 2. Geochronology and stratigraphic context of the fossil sites. A, The Pennsylvanian Timescale (compiled from Peterson 2011; Waters and Condon 2012; Pointon *et al.* 2012; Richards 2013). B, Stratigraphy of the Pennsylvanian (Bashkirian) Cumberland Group and Pennsylvanian (Moscovian) Pictou Group of Atlantic Canada (modified from Gibling *et al.* 2008; Bashforth *et al.* 2014) showing the presence of Langsettian marine bands documented in the Joggins (Grey *et al.* 2011) and Tynemouth Creek (Falcon-Lang *et al.* 2015*b*) formations, and the new marine band (reported here) from the early to mid-Bolsovian part of the Minto Formation. Fig. 2 set for double column (166 mm).

FIG. 3. Geology of the Pennsylvanian (early Bolsovian) Minto Coalfield (modified from Hacquebard and Barss 1970). A, Isopachytes for (i) the Minto Coal and (ii) coal to basement, the latter indicating onlap towards the northeast. B, Sandstone/mudstone ratio in the roof rock of the Minto Coal showing NE-SW trending drainage channels that, locally, ‘wash out’ the coal (i.e., areas where Minto Coal is eroded). Fig. 3 set for double column (166 mm).

FIG. 4. Sedimentary context of the fossil sites based on borehole core DH62-1. A, Graphic log of a short section of borehole DH62-1 (core boxes 44–52; depth 196–231 m) illustrating the three units of the Minto Formation (see text for explanation). The Minto Coal is removed from the core and limestone beds are believed to represent a roof facies as seen in the Joggins Formation (Davies and Gibling 2003). B, Erosive-based fluvial channel conglomerate facies in lower unit. C, Pin-stripe lamination in estuarine facies in middle unit. D, Red mudrock with carbonate glaebules in upper unit. E, Close-up of paired mud-drapes in ripple cross-lamination in middle unit, a distinctive tidal indicator (cf. Naylor *et al.* 1998; Costain 2000). Scale bar is 30 mm (B–D), 4 mm (F). Fig. 4 set for double column (166 mm).

FIG. 5. Petrology of limestone Lithology 1 (shallow marine facies at Coal Creek: A–G, NBMG 18789) and Lithology 2 (brackish embayment facies at Iron Bound Cove: H–I, NBMG 18611). A, Punctate brachiopods. B, fish skeletal fragments. C, Ostracodes. D, Punctate brachiopods and possible sponge spicules. E, Spirorbiform microconchids. F, Echinoderm spine mineralised with framboidal pyrite. G, putative foraminifera. H, Bivalves. I. Bivalves and phosphatic (francolite) nodule possibly of fish origin. Abbreviations: bv, bivalve fragment; es, echinoid spines; f, foraminifera test; fb, fish skeletal fragments; fp, framboidal pyrite; os, ostracode carapace; pb, punctate brachiopods; pn, phosphatic nodule, sp, spirorbiform microconchids; Scale bar is 1 mm (A–D, H–I), 0.5 mm (E–F), 0.25 mm (G). Fig. 5 set for double column (166 mm).

FIG. 6. Macroscopic invertebrates found in Lithology 2 (brackish embayment facies at Coal Creek). A, Spirorbiform microconchid, NBMG 15841. B, Abundant spirorbiform microconchids, NBMG 15815. C, Articulated *Naiadites* bivalves, NBMG 19967. Abbreviations: sm, spirorbiform microconchids. Scale bar is 1 mm (A), 1.5 mm (B), 5 mm (C). Fig. 6 set for double column (166 mm).

FIG. 7. Sedimentary and fossil characteristics of Lithology 3 (tidal estuary facies). A,

Symmetrically-rippled siltstone to very fine-grained sandstone showing fish skeletal fragments concentrated within mud-rich ripple troughs. NBMG 15901 (specimen dissolved to extract fish fauna). B, Enlargement of area in (A) showing *Orthacanthus* tooth and macerated skeletal debris. Abbreviation: xt, xenacanthid tooth. Scale bar as indicated (ruler divided into 10 mm intervals) for A; 10 mm for B. Fig. 7 set for double column (166 mm).

FIG. 8. Tip heaps adjacent to the former opencast mine at Iron Bound Cove (flooded area on the right; Latitude 46°08.67'N; Longitude 65°58.10'W), illustrating how material was collected by 'surface prospecting'. Fig. 8 set for single column (80 mm).

FIG. 9. Teeth of Chondrichthyans from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–D, Tricuspid tooth of *Orthacanthus compressus*, NBMG 19617, in aboral (A), oral (B), dorso-aboral (C), and ventro-oral (D) views. E, Tooth of Xenacanth indet., NBMG 19629. F, Denticle of elasmobranch indet., NBMG 19667. G, Denticle of elasmobranch indet., NBMG 19647. H–J, Teeth of *Ageleodus pectinatus*: NBMG 19613 in aboral view (H), NBMG 19613 in oral view (I) and NBMG 15175 in aboral view (J). Abbreviations: cb, coronal button; nf, nutrient foramen; mf, median foramen. Scale bar is 2 mm (A–D), 1 mm (E), 0.25 mm (F–G), 0.5 mm (H–I), 2 mm (J). Fig. 9 set for double column (166 mm).

FIG. 10. Size ranges for Chondrichthyan teeth from the Minto Formation (Pennsylvanian), New Brunswick. A, Range of heights and frequencies for teeth of *Orthacanthus*. B, Cusp counts and frequencies for complete teeth of *Ageleodus*. Figure 10 set for single column (80 mm).

FIG. 11. Spines of the Acanthodians from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–F, *Gyracanthides* sp., G–H, *Acanthodes* sp. A–C, spines in lateral view: NBMG 15173 (A), NBMG 10739/1 (B), with indications of location of close-ups D and E, and NBMG 10739/2 (C). D, Striae on the insertion area and the angle between the striae

and the exsertion area, NBMG 10739/1. E, Chevron pattern in ornament ridges on the leading edge, NBMG 10739/2. F, cross-section of a spine, NBMG 10739/4. G, spine in lateral view, NMBG 15174. H, spine in lateral view, NBMG 15852. Line at r-s represents the insertion/exsertion boundary (IEB). Line at x-y represents a line perpendicular to the leading edge. Scale bar is 20 mm (B, C), 10 mm (A, G, and H), 2 mm (F), 1 mm (D and E). Fig. 11 set for double column (166 mm).

FIG. 12. Feeding plates of Dipnoans from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A–B, Feeding plate of *Ctenodus interruptus*, NBMG 10740 (A), with close-ups of isolated xenacanth teeth sitting on the surface (B). C–D, Fragments of the feeding plates of Dipnoi indet., NBMG 18609 showing convergent ridges (C), and NBMG 19699, showing differential apical elongations (D). Scale bar is 4 mm (A), 1 mm (B–D). Fig. 12 set for single column (80 mm).

FIG. 13. Teeth and scales of Rhizodonts and Tetrapodomorphs from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A, Tooth of *Strepsodus sauroides*: NBMG 15820 in lateral view. B, C, Tooth of *Archichthys portlocki*, NBMG 19972, showing striations, in lateral view (B), and plication count on the base (C). D–E, Scales of cf. *Archichthys portlocki*, NBMG 19689 (D), NBMG 15831 (E). F, Tooth of cf. *Rhizodus hibberti* NBMG 15809. G, Scale of cf. *Rhizodopsis sauroides* NBMG 15901 showing the attachment side. H–J, Scales of *Megalichthys* indet.: NBMG 10741/1, showing the free field (H), and close-up image of the cosmine cover of the free field (I), and NBMG 19974a, showing the attached surface (J). K–L, Centrum of *Megalichthys* sp. NBMG 19958, in articular (K) and lateral (L) views. M–N, Teeth of Tetrapodomorpha indet., NBMG 10776 (M), and NBMG 10777 (N). Scale bar is 2 mm (A–C, M, and N); 20 mm (F), 10 mm (D–E, G, K, and L), 20 mm (H, J), separate 2 mm scale bar (I). Fig. 13 set for double column (166 mm).

FIG. 14. Tetrapod remains, with provisional identifications. A, Small dentary of a possible ?colosteid bearing teeth, NBMG 15821. B, C, intecentrum of a possible embolomerous anthracosaur vertebra, in ?anterior (B) and lateral (C) views, NBMG 15783, and D, small tetrapod limb bone (NBMG 15915). Scale bar is 80 mm (A), 10 mm (B–C), 7.5 mm (D). Fig. 14 set for single column (80 mm).

FIG. 15. Actinopterygian remains from the Minto Formation (Pennsylvanian) of New Brunswick, Canada. A, Eurynotiform, B – E, indeterminate actinopterygians. A, jaw fragment with five teeth, NBMG 20021. B–C, Scale, NBMG 19679/1 showing the free field (B), and the attached surface (C). D, Sculptured scale or dermal skull bone, NBMG 19804a. E, Tooth, NBMG 19684. F, Vertebra, NBMG 19686. Abbreviations: las, lateral attachment site; vr, ventral ridge. Scale bar is 0.4 mm (A, F), 0.5 mm (B–C, and E). Fig. 15 set for single (80 mm).

FIG. 16. Fish coprolites (bromalites). A, Heteropolar microspiral coprolite, NBMG 19979. showing coils and posterior spire. B, Thin section of heteropolar microspiral coprolite containing fish skeletal fragments including probable juvenile xenacanthid tooth (box: F), NBMG 18789. C, Large, short cylindrical coprolite composed of calcareous material (box: E), NBMG 20000. D, Rounded, bilobed coprolite (box: G), NBMG 19824. E, Expanded view of spirorbiform microconchids and bivalve fragments in coprolite shown (C), NBMG 20000. F, Expanded view of xenacanthid tooth in coprolite (B), NBMG 18789. G, Expanded view of rhizodont tooth and actinopterygian scale (D), NBMG 18789. Abbreviations: as, actinoptergian scale; bf, bivalve fragments; ps, posterior spiral; rt, rhizodont tooth; sm, spirorbiform microconchids; xt, xenacanthid tooth. Scale bars are 4 mm (A–B, D), 6 mm (C), 1.5 mm (E), 1 mm (F, G). Fig. 16 set for single (80 mm).

FIG. 17. Summary of 10 fish faunas from brackish-marine facies in the Carboniferous Maritimes Basin of Atlantic Canada. Carboniferous timescale based on critical synthesis of

recent papers (Peterson 2011; Waters and Condon 2012; Pointon *et al.* 2012; Richards 2013) and age of key formations in the Maritimes Basin based on various sources (e.g., Calder 1998; Gibling *et al.* 2008 for discussion). Faunas based on illustrations in published records, revised in light of modern nomenclature. Principal sources for the compilation (Dawson 1868; Gardiner 1966; Carroll *et al.* 1972; Calder 1998) were supplemented by the following additional sources (Lambe 1910; Baird 1962, 1978; Greiner 1977; Johnson 1979, 1999; Miller and McGovern 1997; Turner *et al.* 2005; Brazeau 2005; Jeffrey 2006; Sues *et al.* 2013; Mansky and Lucas 2013; Carpenter *et al.* 2015; this paper; Yale Peabody Museum collections database: http://collections.peabody.yale.edu/search/). Fig. 17 set for double column (166 mm).

TABLES

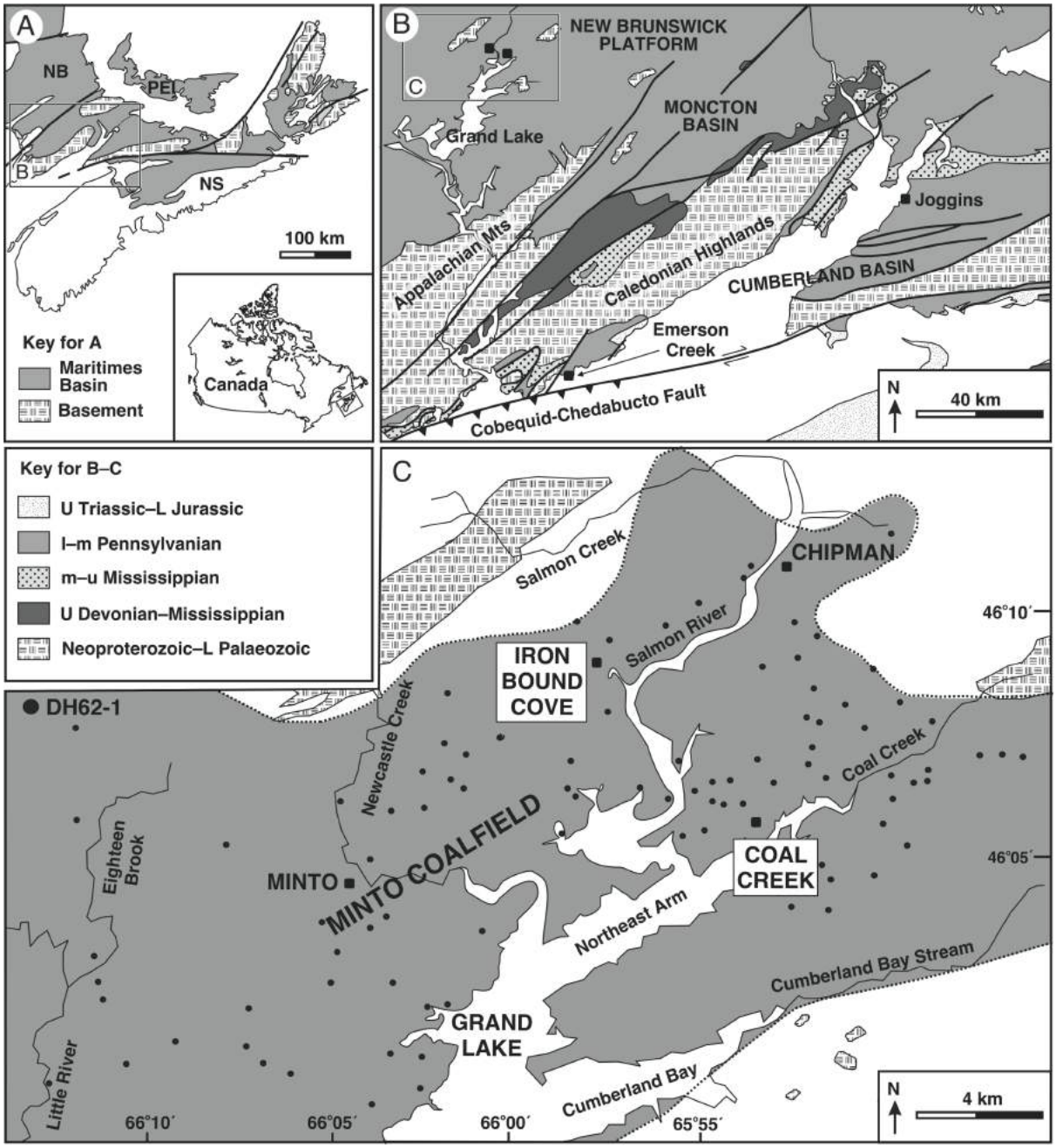
Table 1. Summary of fish taxa from the Pennsylvanian (early Moscovian; early Bolsolvian) Minto Formation of New Brunswick, Canada (cf. Bashkirian fish fauna in Joggins Formation; Carpenter *et al.* 2015, fig. 5).

- Class CHONDRICHTHYES
  - Subclass ELASMOBRANCHII
    - Superorder XENACANTHIMORPHA
      - Order XENACANTHIFORMES
        - Family DIPLODOSELACHIDAE
          - Genus *ORTHACANTHUS*
            - ***Orthacanthus compressus***
      - Order *incertae sedis*
        - Family *incertae sedis*
          - Genus *AGELEODUS*
            - ***Ageleodus pectinatus***
- Class ACANTHODII Owen, 1846
  - Order *incertae sedis*
    - Family GYRACANTHIDAE
      - Genus *GYRACANTHIDES*
        - ***Gyracanthides* sp.**
  - Order ACANTHODIDA
    - Family ACANTHODIDAE
      - Genus *ACANTHODES*
        - ***Acanthodes* sp.**
- Class OSTEICHTHYES
  - Subclass SARCOPTERYGII
    - Infraclass DIPNOMORPHA
      - Order DIPNOI
        - Family *incertae sedis*
          - Genus *CTENODUS*
            - ***Ctenodus interruptus***
    - Infraclass TETRAPODOMORPHA
      - Order RHIZODONTIDA
        - Family RHIZODONTIDAE
          - Genus *STREPSODUS*
            - ***Strepsodus sauroides***
          - Genus *ARCHICHTHYS*
            - ***Archichthys portlocki***
          - Genus *RHIZODUS*
            - **cf. *Rhizodus hibberti***
      - Order *incertae sedis*
        - Family RHIZODOPSIDAE
          - Genus *RHIZODOPSIS*
            - **cf. *Rhizodopsis sauroides***

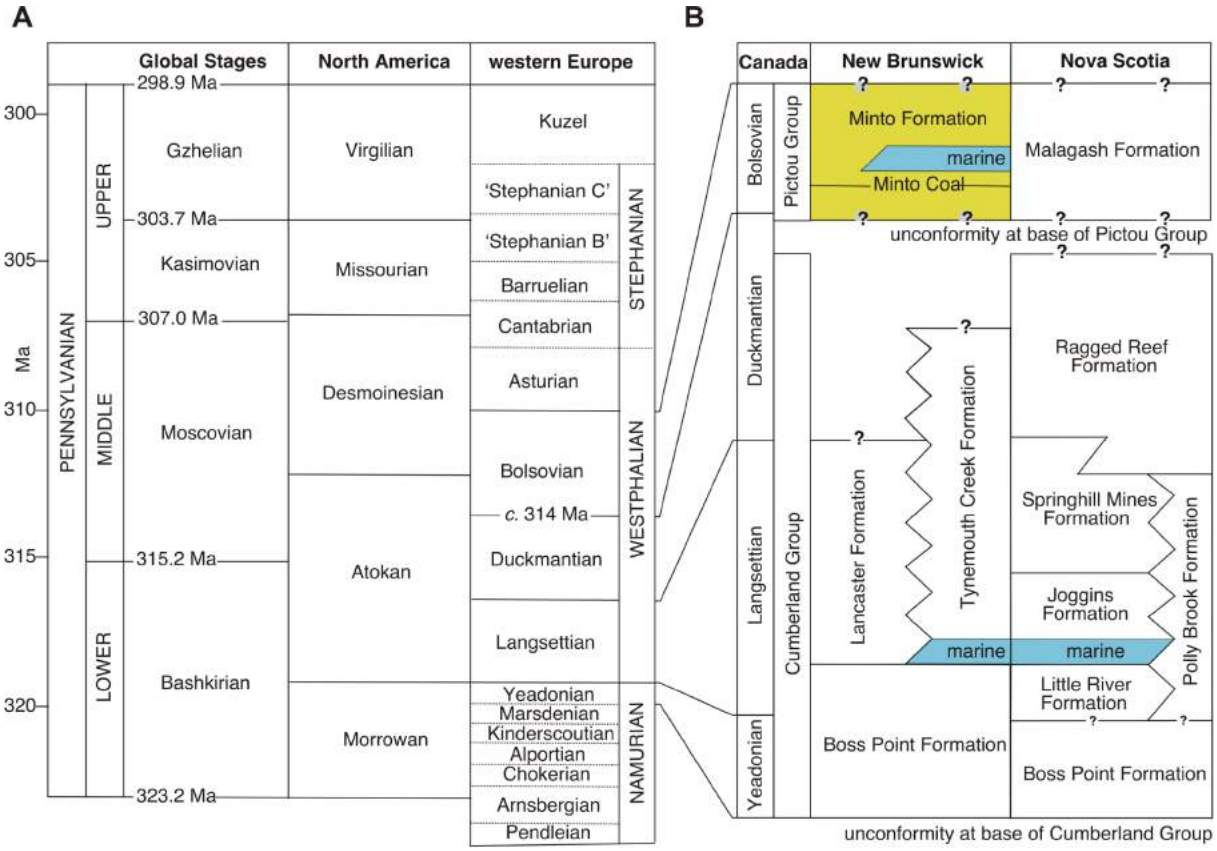
Order Sarcopterygii *incertae sedis*
Family MEGALICHTHYIDAE
Genus *MEGALICHTHYS*
***Megalichthys* sp.**
Subclass ACTINOPTERYGII Cope, 1887
Order EURYNOTIFORMES
Actinopterygii indet.

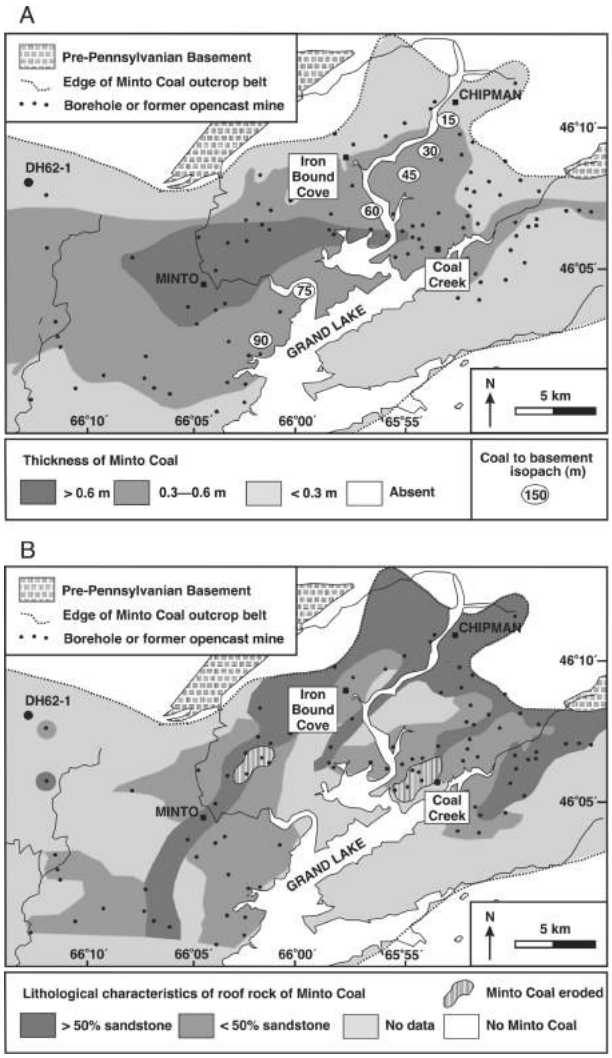
Table 2. Quantitative data for the facies distribution of fish specimen ranked at class/order and generic level. Note that the number of specimens at class/order level (n = 325) is higher than at generic level (n = 181) because some specimens can be assigned to class/order but not to genus. Percentage values at class/order and genus level differ because of they are based on these different datasets. The inverse of the Simpson Index (1 – H) is calculated for generic level data only.

Palaeoenvironment	**Number of specimens**	**Shallow marine**	**Brackish embayment**	**Brackish tidal estuary**	**All facies**
Lithology		1	2	3+4	
Orthacanthus compressus	71	25.0 %	39.2 %	53.3 %	39.2 %
Ageleodus pectinatus	67	18.8 %	44.8 %	23.3 %	37.0%
Chondrichthyes	**209**	**41.9 %**	**65.2 %**	**75.0 %**	**64.3 %**
Gyracanthides sp.	3	6.3 %	1.5 %	0.0 %	1.6 %
Acanthodes sp.	4	0.0 %	1.5 %	0.0 %	1.6 %
Acanthodians	**17**	**3.2 %**	**6.4 %**	**0.0 %**	**5.2 %**
Ctenodus interruptus	2	6.3 %	0.8 %	0.0 %	1.0 %
Archichthys portlocki	5	6.3 %	1.5 %	0.0 %	2.8 %
Strepsodus sauroides	9	6.3 %	5.4 %	3.3 %	5.0 %
cf. *Rhizodus hibberti*	16	6.3 %	5.4 %	16.7 %	8.8 %
cf. *Rhizodopsis sauroides*	1	0.0 %	0.0 %	3.3 %	0.6 %
Megalichthys sp.	5	25.0 %	0.8 %	0.0 %	2.8 %
Sarcopterygians	**59**	**48.4 %**	**13.6 %**	**20.5 %**	**17.8 %**
Actinopterygians	**26**	**6.5 %**	**8.8 %**	**4.5 %**	**8.0 %**
Tetrapods	**15**	**0%**	**6.0%**	**0%**	**4.6%**
1- H for genera		**0.805**	**0.641**	**0.428**	

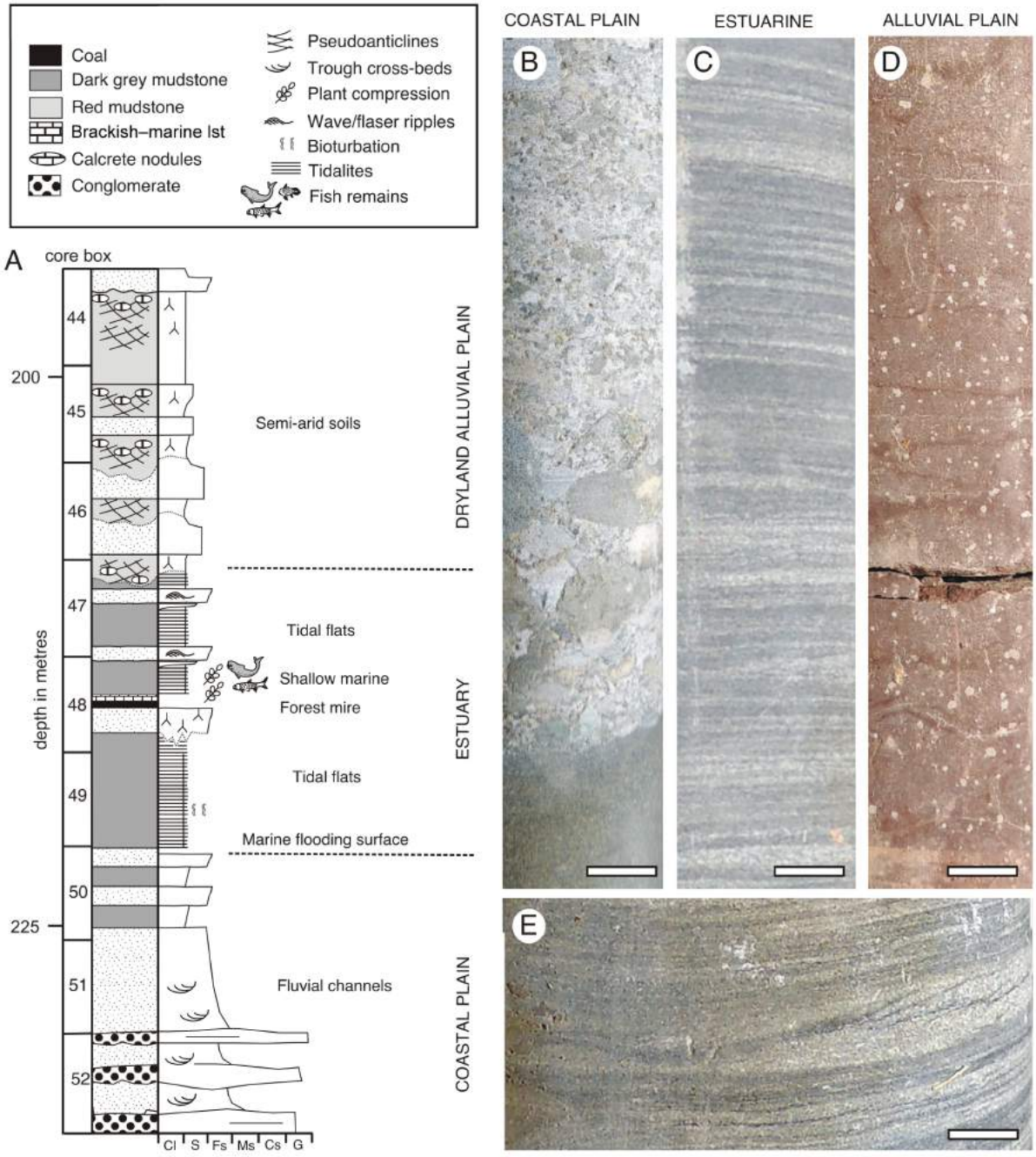

A
NB
PEI
NS
B
100 km
Key for A
Maritimes Basin
Basement
Canada
B
C
NEW BRUNSWICK PLATFORM
MONCTON BASIN
Grand Lake
Joggins
Appalachian Mts
Caledonian Highlands
CUMBERLAND BASIN
Emerson Creek
Cobequid-Chedabucto Fault
N
40 km
Key for B–C
U Triassic–L Jurassic
l–m Pennsylvanian
m–u Mississippian
U Devonian–Mississippian
Neoproterozoic–L Palaeozoic
C
Salmon Creek
CHIPMAN
46°10′
Salmon River
IRON BOUND COVE
DH62-1
Newcastle Creek
Coal Creek
Eighteen Brook
MINTO
MINTO COALFIELD
COAL CREEK
46°05′
Northeast Arm
Cumberland Bay Stream
GRAND LAKE
Little River
66°10′
66°05′
66°00′
Cumberland Bay
65°55′
N
4 km

1894
1895

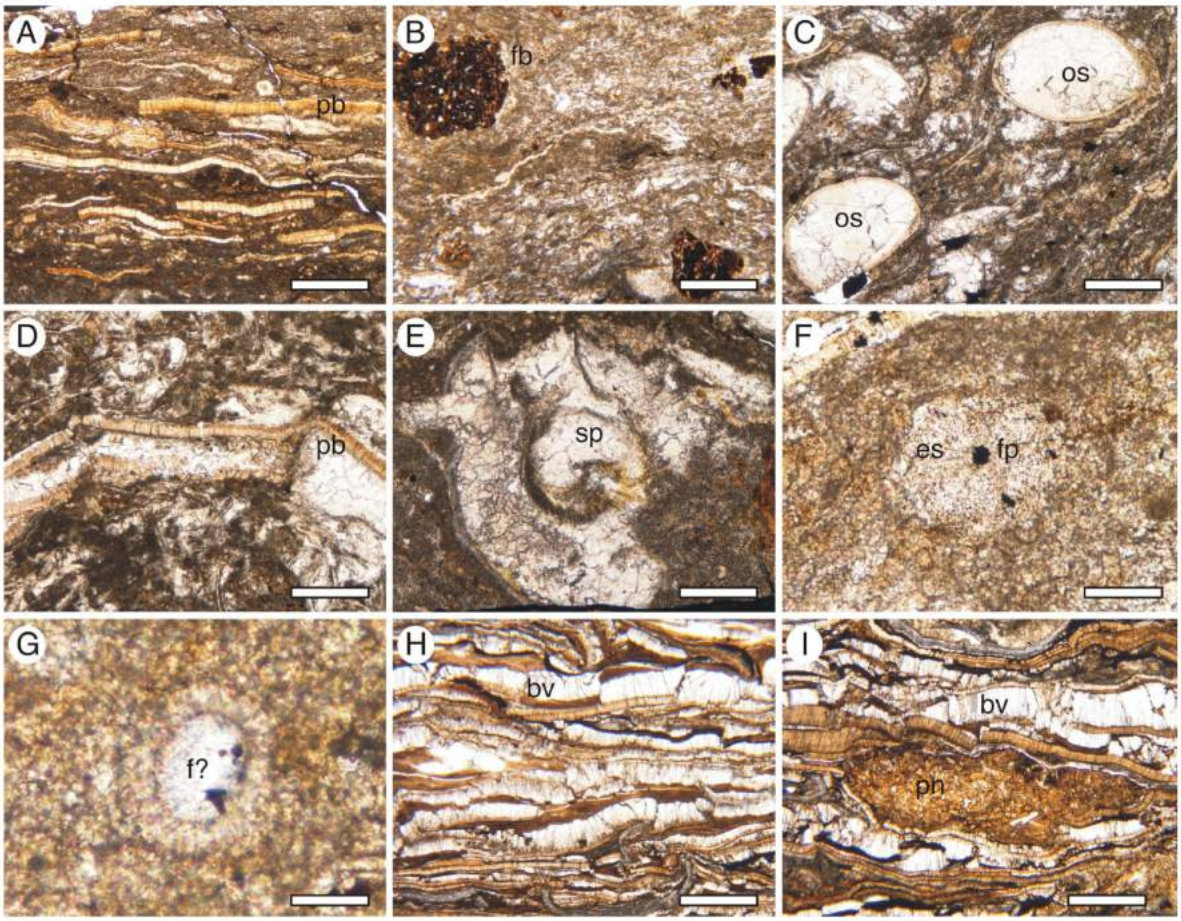

A
Global Stages
North America
western Europe
298.9 Ma
300
Gzhelian
Virgilian
Kuzel
'Stephanian C'
303.7 Ma
'Stephanian B'
305
Kasimovian
Missourian
Barruelian
307.0 Ma
Cantabrian
Desmoinesian
Asturian
Ma
310
Moscovian
Bolsovian
c. 314 Ma
315
315.2 Ma
Atokan
Duckmantian
Langsettian
Bashkirian
320
Yeadonian
Marsdenian
Kinderscoutian
Morrowan
Alportian
Chokerian
323.2 Ma
Arnsbergian
Pendleian
PENNSYLVANIAN
UPPER
MIDDLE
LOWER
STEPHANIAN
WESTPHALIAN
NAMURIAN
B
Canada
New Brunswick
Nova Scotia
Bolsovian
Pictou Group
Minto Formation
marine
Minto Coal
Malagash Formation
unconformity at base of Pictou Group
Duckmantian
Cumberland Group
Ragged Reef Formation
Lancaster Formation
Tynemouth Creek Formation
Springhill Mines Formation
Joggins Formation
Polly Brook Formation
Langsettian
marine
marine
Little River Formation
Yeadonian
Boss Point Formation
Boss Point Formation
unconformity at base of Cumberland Group


A
Pre-Pennsylvanian Basement
Edge of Minto Coal outcrop belt
Borehole or former opencast mine
CHIPMAN
46°10'
DH62-1
Iron Bound Cove
15
30
45
60
Coal Creek
46°05'
MINTO
75
GRAND LAKE
90
N
5 km
66°10'
66°05'
66°00'
65°55'
Thickness of Minto Coal
> 0.6 m
0.3—0.6 m
< 0.3 m
Absent
Coal to basement isopach (m)
150
B
Pre-Pennsylvanian Basement
Edge of Minto Coal outcrop belt
Borehole or former opencast mine
CHIPMAN
46°10'
DH62-1
Iron Bound Cove
Coal Creek
46°05'
MINTO
GRAND LAKE
N
5 km
66°10'
66°05'
66°00'
65°55'
Lithological characteristics of roof rock of Minto Coal
> 50% sandstone
< 50% sandstone
No data
Minto Coal eroded
No Minto Coal

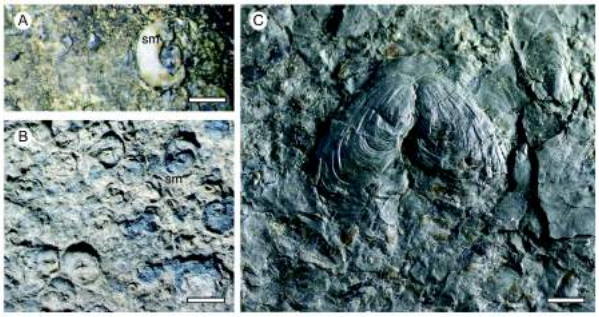
1898
1899


Coal
Dark grey mudstone
Red mudstone
Brackish–marine lst
Calcrete nodules
Conglomerate
Pseudoanticlines
Trough cross-beds
Plant compression
Wave/flaser ripples
Bioturbation
Tidalites
Fish remains
A
core box
depth in metres
200
225
44
45
46
47
48
49
50
51
52
Semi-arid soils
Tidal flats
Shallow marine
Forest mire
Tidal flats
Marine flooding surface
Fluvial channels
DRYLAND ALLUVIAL PLAIN
ESTUARY
COASTAL PLAIN
Cl
S
Fs
Ms
Cs
G
COASTAL PLAIN
ESTUARINE
ALLUVIAL PLAIN
B
C
D
E

1900
1901



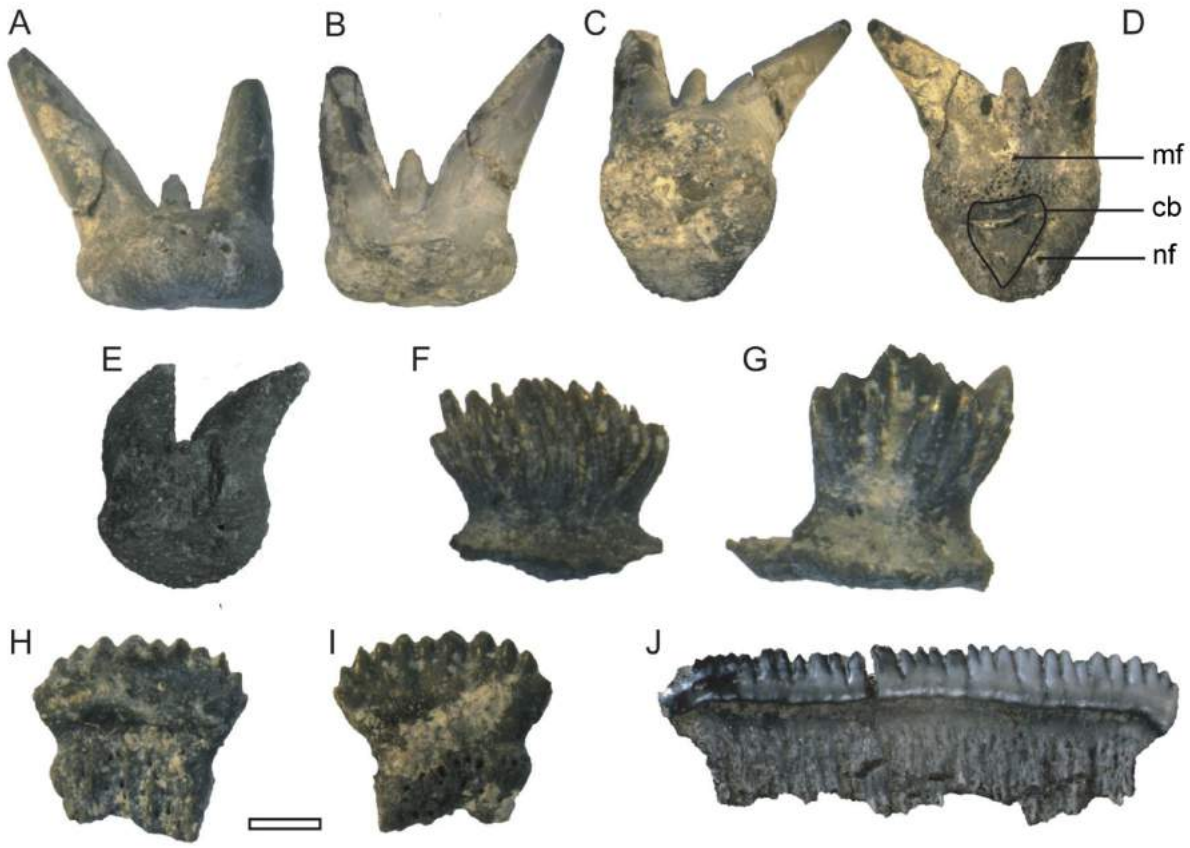
1902



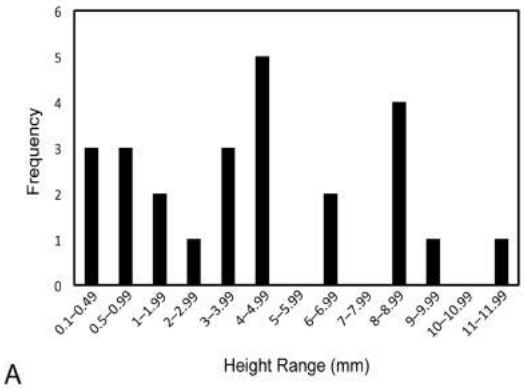
1903

1904

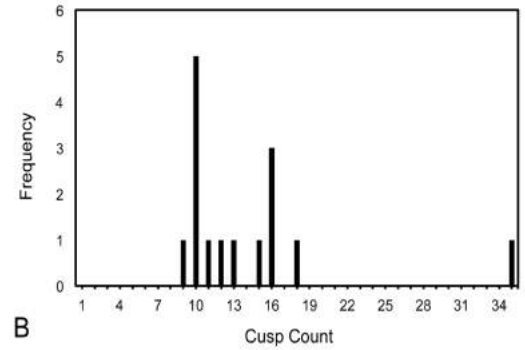
1905



1906

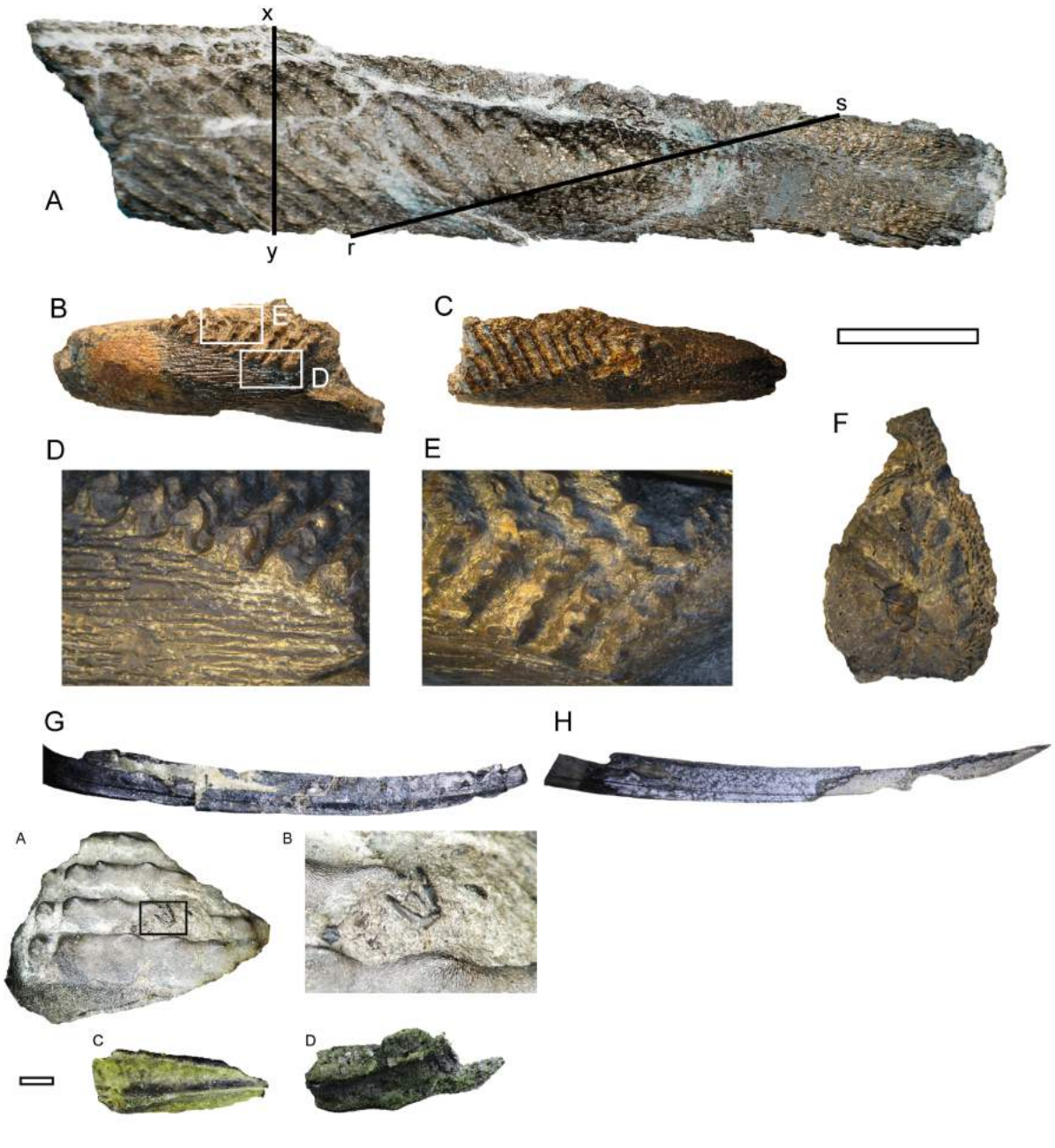


A



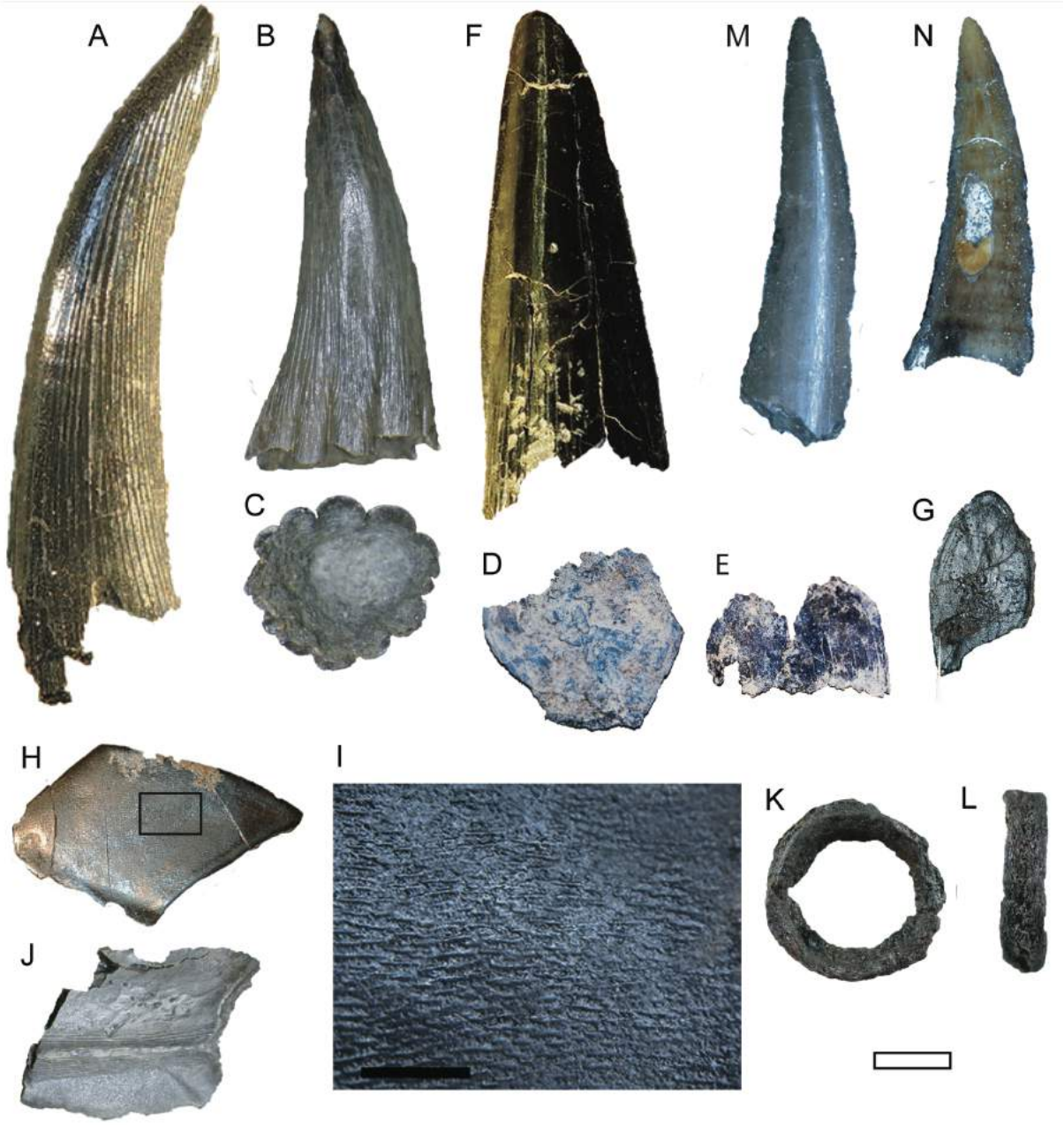
B

1907
1908

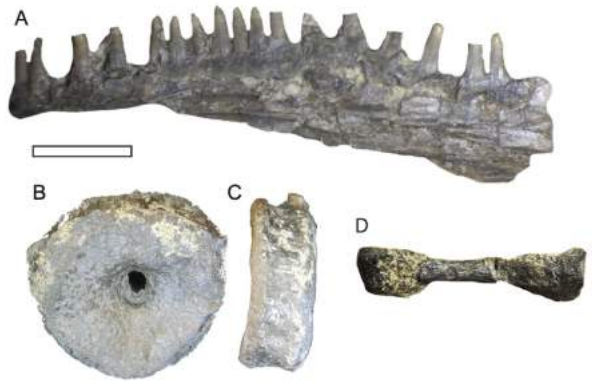


1909

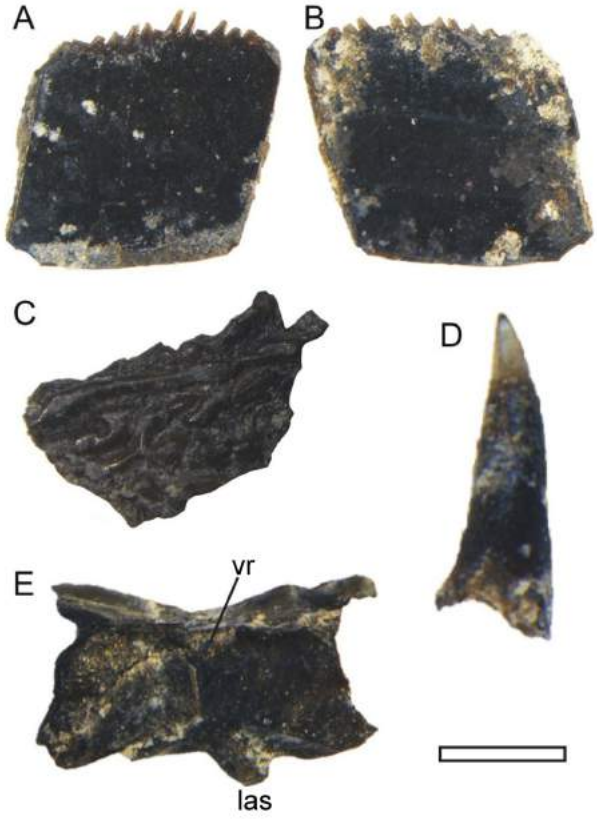
1910
1911



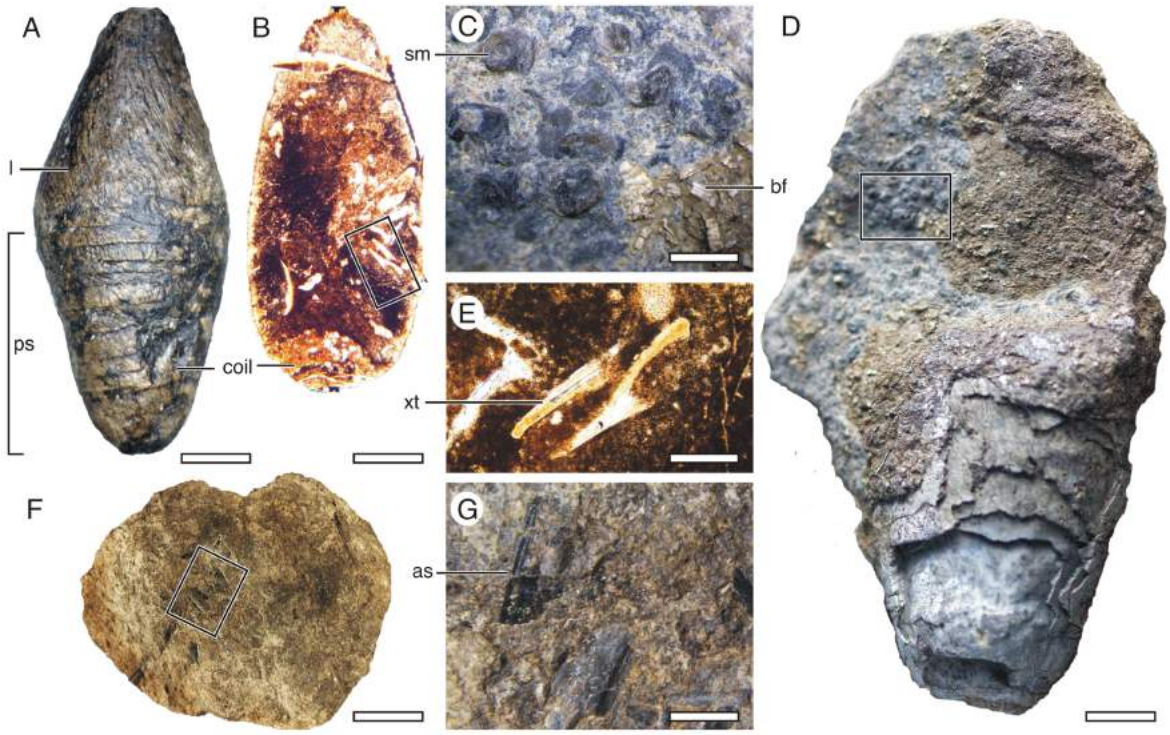
1912
1913



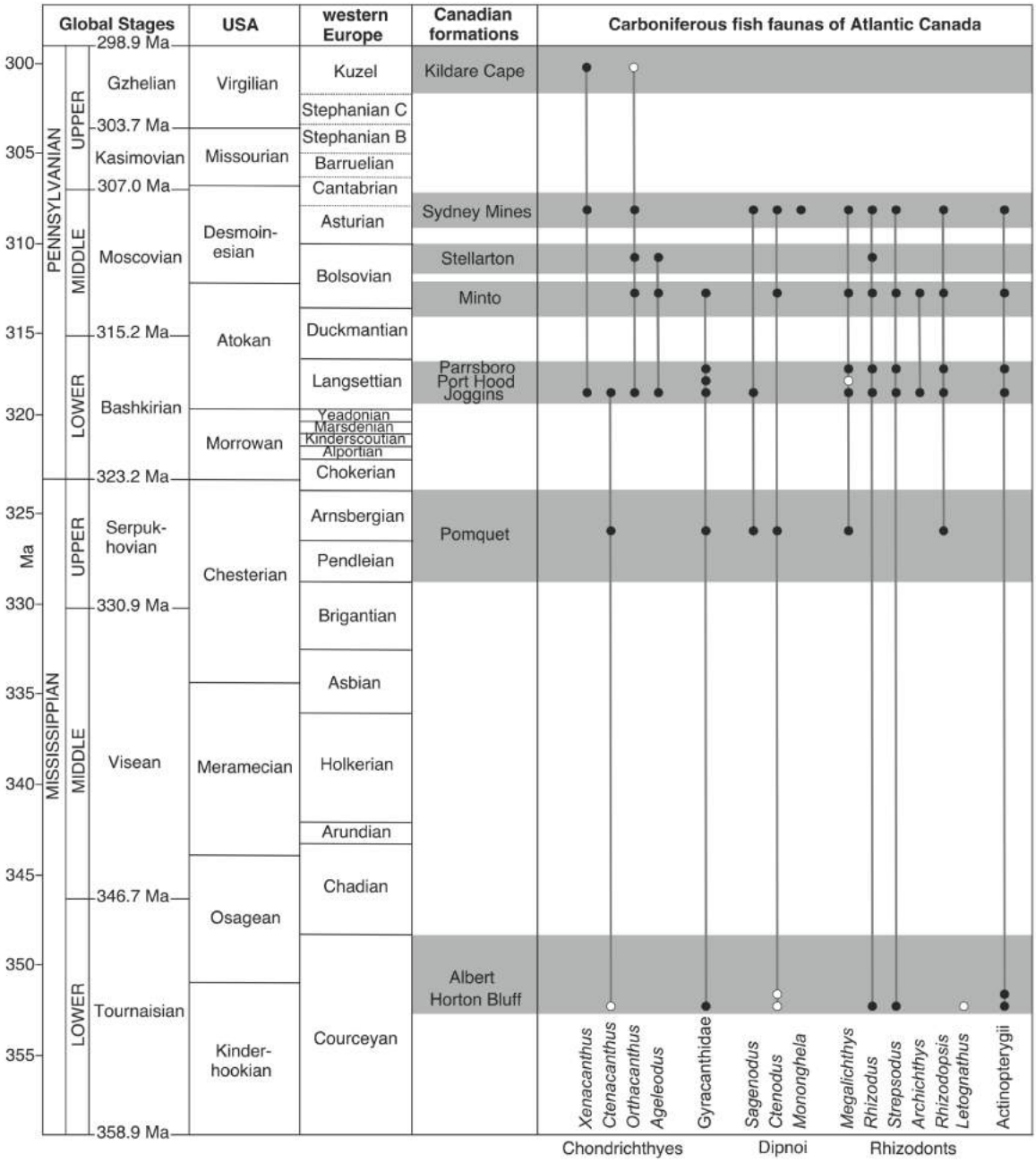
1914



1915



1916


Global Stages
USA
western Europe
Canadian formations
Carboniferous fish faunas of Atlantic Canada
298.9 Ma
Gzhelian
Virgilian
Kuzel
Kildare Cape
Stephanian C
303.7 Ma
Stephanian B
Kasimovian
Missourian
Barruelian
307.0 Ma
Cantabrian
Asturian
Sydney Mines
Desmoin-esian
Moscovian
Bolsovian
Stellarton
Minto
315.2 Ma
Atokan
Duckmantian
Langsettian
Parrsboro
Port Hood
Joggins
Bashkirian
Yeadonian
Marsdenian
Kinderscoutian
Alportian
Morrowan
Chokerian
323.2 Ma
Arnsbergian
Serpuk-hovian
Chesterian
Pomquet
Pendleian
Ma
330.9 Ma
Brigantian
Asbian
Visean
Meramecian
Holkerian
Arundian
Chadian
346.7 Ma
Osagean
Albert
Horton Bluff
Tournaisian
Kinder-hookian
Courceyan
358.9 Ma
PENNSYLVANIAN
MISSISSIPPIAN
UPPER
MIDDLE
LOWER
300
305
310
315
320
325
330
335
340
345
350
355
Xenacanthus
Ctenacanthus
Orthacanthus
Ageleodus
Gyracanthidae
Sagenodus
Ctenodus
Mononghela
Megalichthys
Rhizodus
Strepsodus
Archichthys
Rhizodopsis
Letognathus
Actinopterygii
Chondrichthyes
Dipnoi
Rhizodonts

1917